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APOGAMY IN NEPHRODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **109**

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(WITH PLATES IX AND X, AND THREE TEXT FIGURES)

Introduction

The term apogamy was proposed by DE BARY in 1878, following FARLOW'S discovery (**21, 22**) that in *Pteris cretica*, under artificial culture, the sporophyte is developed from the gametophyte with the suppression of the sexual act. Since this discovery, the apogamous development of a sporophyte as a vegetative outgrowth from the gametophyte in pteridophytes, together with the phenomena of parthenogenesis, where the sporophyte is developed from an unfertilized egg, has been described in many forms.

FARLOW (**22**), in contrasting the apogamous embryo with the normal one, notes the following four points: (1) the apogamous embryo is intimately connected with the prothallium in such a way that one cannot decide where the one begins and the other ends; (2) there is formed no foot or equivalent organ; (3) the vascular bundle of the sporophyte is in direct connection with vessels which lie wholly in the prothallium; (4) the order of evolution is different, a leaf arising first and becoming tolerably well developed before the root and afterward the stem make their appearance.

FARLOW'S investigation was followed by an extensive study of DE BARY (**1**) on a number of forms in Polypodiaceae, in which he described a similar sporophytic growth in *Aspidium Filix-mas cristatum* and *A. falcatum*. He records various conditions of the development of sexual organs in apogamous prothallia: in *Aspidium*

Filix-mas cristatum archegonia are apparently absent, in *Pteris cretica* they never fully developed; although all prothallia bear more or less numerous antheridia.

SADEBECK in the following year reported apogamy in *Todea africana* (in SCHENK'S *Handbuch der Botanik* **1**:233. 1879). And later apogamy was found in *Osmunda regalis* and *Ceratopteris* (LEITGEB **38**); *Todea rivularis*, *T. pellucida* (STANGE **63**); *Doodya caudata* (STANGE **63**, HEIM **29**); *Trichomanes alatum* (BOWER **6**); *Selaginella rupestris* (LYON **43**); *Trichomanes Krausii*, *Pellaea flavens*, *P. nivea*, *P. tenera*, *Notochlaena Eckloniana*, *N. sinuata*, *N. Marantae*, *Gymnogramme farinifera* (WORONIN **78**, **79**); and in some others.

LANG'S study (**36**) of the apogamous development of the sporophytes on prothallia of several forms of Polypodiaceae is the most detailed contribution on apogamy in pteridophytes. The paper presents a discussion of the phenomenon in relation to alternation of generations, and adds detailed descriptions of the results of cultivating prothallia grown from spores, for a period of two years and a half in the following fourteen forms: *Aspidium aculeatum* Sw. var. *multifidum* Woll, *A. angulare* Willd. var. *foliosum multifidum*, var. *acutifolium multifidum* (no apogamy seen), *A. frondosum* Lowe; *Athyrium nipponicum* Mett., var. *cristatum*, *A. Filix-foemina* Bernh. var. *percristatum* Cousens, var. *cruciato-cristatum*, var. *coronatum* Lowe; *Nephrodium dilatatum* Desv. var. *cristatum gracile*, *N. Oreopteris* var. *coronans* Barnes; *Polypodium vulgare* L. var. *grandiceps* Fox; *Scolopendrium vulgare* Sm. var. *ramulosissimum* Woll, var. *marginale*.

According to his account, the apogamous growth resulted from artificial cultures, watered entirely from below and exposed to direct sunlight, important departures from the normal conditions surrounding fern prothallia. The asexual sporophytic outgrowth from the prothallia present some minor differences in different individuals, but, taken as a whole, they arose in the following ways: as leaves, roots, and ramenta directly on the prothallia or on a cylindrical process from the prothallium; as a continuation of the process as a leaf; as sporangia on the process from the prothallium; as tracheids in the prothallia or in the middle lobe and cylindrical process.

It seems hard to draw from these experiments any more precise

conclusion than that the normal life-history is checked at a critical period (fertilization) and that the plant is forced into an expression of vegetative activity. Apogamy brings forward also the theory of the homologous origin of alternation as contrasted with the antithetic. The theory of the homologous origin of the alternation of generations, as held by PRINGSHEIM (**55, 56**) and SCOTT (**61**), is discussed by LANG in his studies on apogamy. He is inclined to the opinion that apogamy and apospory in ferns support the homologous view, since the prothallium can so readily take on sporophytic characters and the sporophyte can develop the gametophyte aposporously. He recognized, however, that all speculations on these points must be tentative until the actual nuclear conditions in apogamy and apospory have been ascertained.

The investigations mentioned above have greatly extended our knowledge concerning the phenomena of apogamy and apospory, and some of them have contributed much to elucidate the structural features involved, but cytological details of apogamy in pteridophytes remained unknown until last year, when there appeared two papers, one by FARMER and DIGBY (**24**) and the other by STRASBURGER (**68**).

FARMER and DIGBY'S paper is one of the most important of recent contributions to apogamy in ferns. Their preliminary note (**23**), published four years ago, announced the discovery of nuclear fusions in the vegetative cells previous to the apogamous sporophytic outgrowths from prothallia. The final paper deals with the results of their studies on apogamy and apospory in the following seven forms: *Lastrea pseudo-mas* vars. *polydactyla* Wills., *polydactyla* Dadds, *cristata apospora* Druery; *Athyrium Filix-foemina* vars. *clarissima* Jones, *clarissima* Bolton, and *unco-glomeratum* Stansfield; and *Scolopendrium vulgare* var. *crispum Drummondae*.

All the prothallia of the five forms used for their investigations, excepting the two *polydactyla* varieties, were aposporus outgrowths, either on peripheral cells of unmatured sporangia, from sori of sterile sporangia, or on apices, surface, or margins of pinnae. In two forms —var. *unco-glomeratum* and var. *cristata apospora*—the aposporous prothallia were induced artificially by pegging detached pinnae down on damp soil. The two varieties *polydactyla* of Lastrea, producing ordinary spores and prothallia, were obtained by sowing the spores.

In these apogamous prothallia antheridia are always produced in profusion and sperms are matured in every case, but the development of archegonia is different in different forms: sometimes no archegonia are produced (var. *polydactyla* Wills. and *cristata apospora*), or some are formed but do not attain maturity (var. *clarissima* Jones), and in these two cases sporophytes appeared apogamously as vegetative outgrowths; in other cases an egg is produced in the normal way, but there is no fertilization, the embryo being developed either from the unfertilized egg (var. *clarissima* Bolton and Scolopendrium) or endogenously in connection with an archegonium (*unco-glomeratum* Stansfield).

So far as the number of chromosomes is concerned, these seven cases of apospory and apogamy may be placed in three categories: (1) in the two vars. *polydactyla*, in which sporogenesis shows the ordinary reduction, a doubling of chromosomes is attained by the fusion of vegetative nuclei instead of by fertilization; (2) in four forms—three varieties of *Athyrium Filix-foemina* and a Scolopendrium—sporogenesis is omitted from the life-cycle, prothallia arise directly from abortive sporangia or pinnae, and sporophytes develop apogamously from the prothallia, the approximate sporophytic number of chromosomes being retained throughout the cycle; (3) in var. *cristata apospora*, in which apospory and apogamy regularly follow each other, the approximate number of chromosomes through the life-cycle is 60, and the authors believe that in this case the sporophyte may retain the original gametophytic number of chromosomes, the suggestion being based upon the fact that the number 60 approximates 72, the gametophyte number of the type species *Lastrea pseudo-mas*.

Throughout the investigation the authors met a variable number of chromosomes in different parts of an individual, and they express the belief that such variations are not due entirely to errors of counting, but that they correspond to fluctuations in the number actually present in the different regions. Their general conclusions are as follows: there is no necessary correlation between the periodic reduction in the number of chromosomes and the alternation of generations. Fertilization and reduction, however, are recognized as holding a very definite relation to one another, but without any *a priori* grounds for assuming any necessary connection between either of them and any other

feature in the life-history; and therefore the problem of alternation must be settled by an appeal to evidence other than that derived from the facts of mitosis.

STRASBURGER (**68**) studied apogamy in Marsilia from the cytological standpoint. Previous to his work, parthenogenesis in Marsilia had been described by two observers. Almost ten years ago SHAW (**62**) found normal parthenogenesis, as it was called by the author, to be of frequent occurrence. He also isolated megaspores of *Marsilia Drummondii* from microspores before the sperms matured, and over 50 per cent. of the isolated female prothallia produced embryos, while not more than 69 per cent. of those which were mixed with male prothallia produced embryos. Four years later NATHANSOHN (**48**) induced parthenogenesis in *Marsilia vestita* and *M. macra*. He found that it was possible to stimulate the egg cell to a parthenogenetic development by exposing the germinating megaspores to a temperature of 35° C. for 24 hours, and allowing them to continue their development at a temperature of 27° C. As a result, about 7–12 per cent. of the spores gave rise to parthenogenetic embryos. Under lower temperatures the egg developed an embryo only after fertilization. No nuclear conditions were noted by SHAW or NATHANSOHN.

In parthenogenesis in seed plants, a reduction of chromosomes does not occur in the formation of the embryo sac, so that the egg nucleus contains the diploid number, which naturally obviates any necessity for the act of fertilization. Considering parthenogenesis in seed plants, there arises naturally a question as to how the egg nucleus in Marsilia, which usually establishes a new sporophyte after a normal act of fertilization, could have developed parthenogenetically into the sporophyte. A clear explanation of this question from the cytological standpoint was made by STRASBURGER in his recent paper (**68**).

STRASBURGER states that the classification into species in Marsilia cannot always be relied upon. He finds that megaspores of BRAUN'S *Marsilia Drummondii* develop embryos habitually by parthenogenesis, and that in three species—*M. vestita*, *M. aegyptica*, and *M. quadrifolia*—embryos are formed only after fertilization.

In *Marsilia Drummondii* he finds that the nuclei of the prothallia in the megaspores contain 32 chromosomes, the diploid number, as found in the root tips and other vegetative structures of the sporophyte.

One or two ventral canal cells always persist without disorganizing, which may also prevent the entrance of sperms and check the act of fertilization.

In *Marsilia vestita*, the species worked by NATHANSOHN, STRASBURGER tried NATHANSOHN'S method of inducing parthenogenetic growth, but did not obtain a single parthenogenetic embryo. In this species the sporophytic number 32 is reduced to 16 in sporogenesis, and hence under natural conditions an embryo should develop only after fertilization. He found similar normal conditions in *M. quadrifolia*, *M. elata*, and *M. hirsuta*, whose chromosome number is the same as that of *M. vestita*.

According to his detailed account of sporogenesis in *Marsilia Drummondii*, the number of megaspore mother cells is less than 16, the usual number in normal forms, and sometimes only four. In diakinesis 32 chromosomes appear, and in the metaphase there were observed two kinds of mitotic figures, one of heterotypic type with 16 bivalent chromosomes, and the other of vegetative type with 32 univalent chromosomes. In both cases a second division follows, so that two kinds of megaspore tetrads are formed, one with the $2x$ or diploid number of chromosomes, and the other with the x or haploid number. The proportion of these two kinds of spores differs in each individual form; for instance, in GOEBEL'S material he found the megaspores with the diploid number only. In microsporogenesis there was observed a tendency toward forming a heterotypic figure, but no mature sperms developed; two species, *M. macra* and *M. Nardu*, behaved similarly.

Such a megaspore forms a prothallium whose nuclei have the diploid number of chromosomes, which pass to the egg nuclei, so that the sporophytic number of chromosomes is maintained throughout the life-history, as in cases of parthenogenesis known among seed plants; however, the case found in *Marsilia Drummondii* by STRASBURGER, where a tetrad division occurs not accompanied by chromosome reduction, seems to be a condition never described before, because most of the cases of parthenogenesis known in seed plants are characterized by the omission of the tetrad division as well as the accompanying reduction.

STRASBURGER calls the phenomenon in Marsilia apogamy, main-

taining the principle stated in his paper on parthenogenesis in EUALCHEMILLA (**66**), that the asexual development of an embryo from the gametophyte with the diploid number of chromosomes, whether the embryo comes from an egg or a vegetative cell, should be regarded as apogamy; while the term parthenogenesis should be reserved for the asexual development of an egg with the haploid number of chromosomes and consequently capable of being fertilized. WINKLER (**76**) opposed STRASBURGER'S view concerning the application of the terms apogamy and parthenogenesis. The difference of opinion concerns not only the question of terminology, but also involves theoretical views regarding the significance of the number of chromosomes, which will be considered later.

The present investigation on apogamy in *Nephrodium molle* Desv. was undertaken in the hope of adding something to our knowledge concerning the cytological interpretation of the phenomenon of apogamy. As was stated in the preliminary note, the writer was convinced of the necessity of understanding beforehand the nuclear conditions throughout the whole normal life-history of this species. Consequently, first sporogenesis, and second spermatogenesis, oogenesis, and fertilization were studied. These results were published in two preceding papers (**81, 82**).

Material and methods

All of the apogamous prothallia used in this investigation were raised from ordinary spores, secured from the same material used for the study of sporogenesis, which was collected from the greenhouses of the Hull Botanical Laboratory, of Lincoln Park, and of Washington Park, Chicago.

Spores were sown upon sterilized soil consisting of a mixture of vegetable mold and sand, placed in the greenhouse, and kept growing with special care since October 1906. Some of the prothallia presented certain peculiarities, one being different from the rest in the same pots, but in general the differences held no relation to apogamous development. Antheridia and archegonia were produced in profusion. Nuclear conditions in the vegetative cells, as well as in spermatogenesis, oogenesis, and fertilization, were studied

in this material and the results were published in the preceding papers (**81, 82**).

In a number of pots placed in saucers filled with water like the rest, watering from above was avoided and the cultures were exposed to direct sunlight after the prothallia had developed two or three cells. The excessive evaporation from the soil was regulated carefully, so as not to permit condensation on the prothallia, and allow fertilization. Thus the prothallia were kept growing for a long period in dryness and in exposure to direct sunlight, the temperature of the room being kept at 28°–32° C. No fungi or lower algae developed in the pots.

The rate of growth of these prothallia when compared with that of those placed in normal conditions was quite slow. Antheridia appeared earlier than under normal conditions and were very numerous. About five or six weeks after the prothallia of two or three cells were examined, there was observed a peculiar thickening in the cushion region of some of the prothallia which reached the cushion condition earlier than the rest. This thickening was determined afterward to be the initiation of an apogamous sporophytic outgrowth. During the next three or four weeks the growth of the sporophyte was rather rapid, and at the end of that time it had become leafy. Fixation of the prothallia was made during all stages of development.

The killing and fixing of the material, with washing, imbedding, cutting, and staining, were done by the method used in the study of spermatogenesis, oogenesis, and fertilization.

This investigation was begun in October 1906, at the suggestion of Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN, and I wish to express my sincere gratitude to these gentlemen for their kind advice and criticism. I am also under obligation to the other members of the botanical staff for many courtesies.

Description of the apogamous prothallia

VEGETATIVE MITOSIS

The prothallia which produce sporophytic outgrowths apogamously do so under the influence of artificial culture. The mitoses which occur up to the 30–50-celled stage are exactly similar to those in normal prothallia, but beyond that stage the morphological struc-

ture seems to become influenced by the artificial conditions. The growth becomes very slow, and the cells show a tendency to increase greatly in size, while under normal conditions mitosis would occur before such a size had been reached. Probably for this reason mitotic figures are less frequently met during the growth of such prothallia. As the cell increases in size, its nucleus grows large and the mitotic figure is generally larger than in normal prothallia of this species.

It was not difficult to find stages of mitosis in the vegetative cells, and their comparatively large size facilitated the accurate counting of chromosomes. The resting nucleus contains a delicate reticular structure consisting of a mixture of ragged clumps and slender threads of chromatin. Nucleoli with conspicuous peculiarities of form are always present; sometimes there are two to several isolated round nucleoli scattered irregularly within the nucleus, and sometimes part of them are arranged into a group or groups. They are likely to be mistaken for chromatin nucleoli, but after a close examination of serial stages in the development of the chromosome it is clear that they lie entirely free from the chromatin network and do not seem to contribute any material to the chromosomes by direct transformation. Cell contents beside the nucleus and cytoplasm are not so abundant as in normal cases, the cell cavity consisting largely of vacuoles.

In prophase, the spirem is developed from the chromatin reticulum (*fig. 4*) as described for normal prothallia. The metaphase (*fig. 5*) and anaphase (*figs. 6, 7*) show no peculiar deviation from the typical mitosis. The number of chromosomes is 64 (*fig. 8*) or 66. When two daughter nuclei are reconstructed, a cell plate is laid down between them which finally divides the mother cell into two cells. In this material the binucleate condition was seldom observed, so that it may be claimed that the telophase of mitosis in the vegetative cell is always followed by cell division, and that there is no migration of the nucleus of one cell to an adjacent one.

As stated before, mitosis in the vegetative cells of the normal prothallia and in those reproducing apogamously agree except as to the axis of the spindle, which does not hold any regular relation to the surface of the prothallia, the cell walls being laid down in various directions. This is quite contrary to the condition in normal

prothallia, in which, at least up to the appearance of the archegonium initial, the walls are formed somewhat regularly, being more or less perpendicular or parallel to the surface of the prothallium.

SPERMATOGENESIS

Every apogamous prothallium bears antheridia in profusion, the antheridium initial being formed earlier than in normal prothallia of similar size. The formation of the primary spermatogenous cell, which takes place as in normal prothallia, is studied more readily on account of the comparatively large size. The mitoses from the primary spermatogenous cell to the formation of spermatids and sperms showed no deviation from spermatogenesis in normal prothallia. During these mitoses 64 or 66 chromosomes could always be counted. The peculiar structures which were observed within the cytoplasm in the primary spermatogenous cell of the normal prothallia were also present here, but they seemed to be undoubtedly plastids.

The sperms are actively motile and are attracted by 0.01 per cent. solution of sodium malate. From the similarity of the genetic development, morphological structure, and characteristic response to the chemotactic stimulus, it is clear that sperms formed in such prothallia can function when conditions permit.

An irregularity in the axis of mitoses was observed during the cell divisions within the antheridium: in most cases the first wall which divides the primary spermatogenous cell vertically is followed by two or three vertical walls parallel to the first, before any transverse division takes place.

OOGENESIS

While antheridia and functional sperms are formed in abundance, archegonia are rare in these prothallia. The power of forming archegonia seems to be almost suppressed; and the cushion region where archegonia generally arise is very often covered with antheridia instead of archegonia. In extremely rare cases, however, there appears an archegonium initial, from which a central cell is cut off as in normal prothallia. The central cell either remains without any further division and imbedded below a superficial cell, or develops into canal cells and an egg cell, the projecting neck cells being poorly

developed. The central cell, when it remains undivided, grows to a considerable size, with a corresponding increase in the size of its nucleus, which finally assumes a form similar to that of an egg, but it always appears collapsed. When canal cells and egg are formed, they also appear collapsed. The collapsed appearance of the central, canal, and egg cells is likely induced by the artificial treatment of the prothallia rather than by fixing reagents.

Whether the egg in such a collapsed condition is still capable of fertilization, is questionable, but the writer is inclined to believe that it is incapable of functioning. No case of a sperm having entered an egg was found.

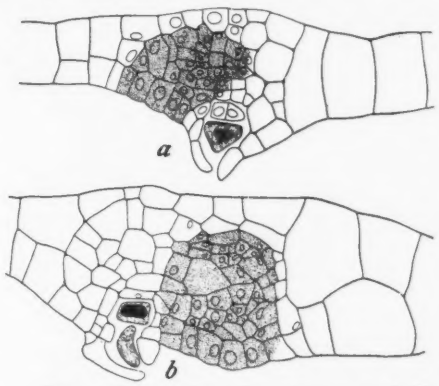

FIG. 1.—Two sections of apogamous prothallia, showing two different stages in the development of archegonia; the shaded regions represent sporophytic outgrowths; *a*, archegonium with central cell; *b*, archegonium with canal cells and egg.

Not only is the formation of archegonia extremely rare, but when formed they are very much belated. In all cases in which their formation was observed, apogamous sporophytic outgrowths were already in an advanced stage of development (*figs. 1a, b*). Hence it is reasonable to suppose that in the apogamous prothallia a tendency to develop sporophytic outgrowths becomes predominant when the power of forming archegonia becomes weak.

SPOROPHYTIC OUTGROWTHS

As described before, during the early development of prothallia, mitoses occur in the vegetative cells just as in normal prothallia, except that the mitotic figures are comparatively large. The mitoses continue in the vegetative cells and there are organized prothallia of a single cell layer in thickness. The general outline of the prothallia does not show any peculiarities which might be regarded as characteristic of apogamous prothallia as distinct from normal ones.

Sporophytic outgrowths begin very early from cells in the region where later the cushion arises, so that the development of the sporophytic outgrowth and the gradual completion of the cushion proceed side by side for a while. When the prothallium has assumed the characteristic heart shape, with a cushion near the sinus and an extensive lateral growth of prothallial tissue on either side, the sporophytic outgrowth is usually in a well-advanced stage. The main features of the formation of this outgrowth and of the gradual completion of the cushion are as follows:

Previous to the formation of the cushion, mitoses take place in rapid succession in the vicinity of the sinus, partition walls always being laid down perpendicular to the surface of the prothallium and parallel to one another, so that the cells formed are very narrow. Some of these mitoses in different stages are represented in *figs. 9–11*. Mitosis continues and cell plates are laid down parallel or oblique to the surface of the prothallium, the ultimate result being the initiation of a thick cushion region (*figs. 12, 13*).

One of the superficial cells in the cushion region begins at once to increase considerably in size, the increase being accompanied by an excessive growth of its nucleus. The nucleus in the resting condition contains a reticulum of ragged clumps and slender threads of chromatin, from which the spirem of the prophase is established (*figs. 14, 14a*). Two or more nucleoli are always present. Successive stages of the mitosis following the early prophase were examined (*figs. 15–17*), which were exactly similar to those of typical mitosis in the vegetative cells of normal prothallia. In the telophase of this mitosis, when the two groups of daughter chromosomes have reached the poles, a little irregularity in the form of the chromosomes is observed, but the number of chromosomes, before they had become aggregated into a mass, was always 64 or 66 (*figs. 18a, b*).

Consequently, it is perfectly clear that, so far as the chromatin is concerned, no change has occurred in the nucleus of these prothallia up to the formation of the superficial cell. In the late telophase a cell plate is laid down perpendicular to the surface of the prothallium, so that there are formed two superficial daughter cells arranged side by side (*fig. 19*).

A number of mitoses follow in the same way, and thus there is

established in a certain region of the superficial layer a group of parallel cells. The increase of the superficial cell is remarkable in apogamous prothallia. In ordinary prothallia, if such a growth in size ever occurs in a superficial cell of the cushion region, it is an archegonium initial; however, the archegonium initial never attains such conspicuous development, surpassing all the other superficial cells in that region. Moreover, the development of the archegonium generally occurs after the cushion region has extended over a comparatively large area and attained some thickness. On the other hand, the increase in size of the superficial cell in an

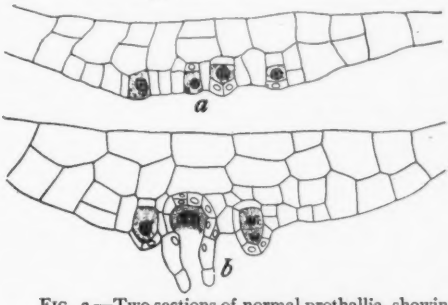

FIG. 2.—Two sections of normal prothallia, showing different stages in the development of archegonia.

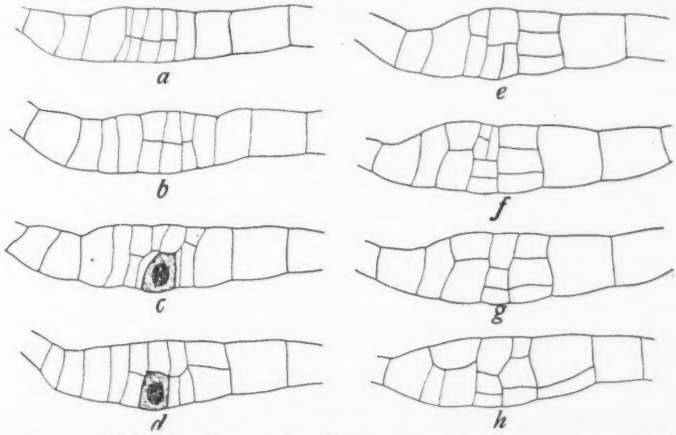

FIG. 3.—Eight successive sections of the same apogamous prothallium showing a single superficial growing to considerable size in a young cushion.

apogamous prothallium commences at an early stage and is associated with the gradual formation of the cushion. The accompanying figures will illustrate the situation. In *fig. 2, a, b* is shown the cushion region, displaying different stages of archegonium development in normal prothallia. *Fig. 3* represents eight successive sections of the same

prothallium, which indicate that a single superficial cell has grown to a considerable size in a young developing cushion region. The remarkable increase in size and the characteristic contents made these cells very conspicuous. Sooner or later, from one of these superficial cells an apical cell is cut off by an oblique wall, and becomes the growing point of a leaf. Sometimes an apical cell appears very early, as shown in *figs. 20* and *21*. During these mitoses, the number of chromosomes is always 64 or 66.

While this process is in progress in the superficial region, cells beneath divide in various directions. Mitoses, of course, occur in various parts during the growth of the prothallia, but they occur more rapidly in the interior region which borders the group of superficial cells whose formation was described above.

Some of the characteristic features that distinguish these interior cells from the other prothallial cells are as follows: they are considerably smaller, probably due to their rapid successive divisions; the nucleus, in spite of the smallness of the cell, is large; the cytoplasmic contents are abundant and the plastids are small and few at this stage.

The mitoses in connection with the formation of this group of interior cells were studied. The general aspect of the mitotic figures in successive stages and the behavior of the chromosomes in these mitoses were similar to those of typical mitosis in the vegetative cells of normal prothallia. It was interesting to notice, however, that the narrowness of the cell cavity and the largeness of the nucleus showed a remarkable resemblance to the condition observed during the development of normal embryos later than the 32-celled stage (*figs. 22–29*). In telophase the number of chromosomes was always 64 or 66 (*fig. 27*).

The mitoses in the groups of superficial and interior cells continue as described above, and there is formed a structure which is in direct connection with the prothallial cells, the structure that later becomes an independent sporophyte. *Figs. 28* and *28a* represent the structure of the sporophytic outgrowth at a certain stage in the course of its development. One apical cell which is already differentiated in the structure is not shown in this section.

Thus the structure of the sporophytic outgrowth is brought about

apparently by the cooperation of the mitoses of two different regions, one of which is a single superficial cell that has attained a conspicuous size, and the other the vegetative cells immediately beneath. If we trace further back the origin of the cells of these regions, they are found to be descendants from the vegetative cell or cells whose sister cells have organized the cushion region. It was impossible to detect a distinct period in which any change had occurred in the chromatin condition up to this development of the sporophytic outgrowth; practically the nucleus of the gametophyte has become directly the nucleus of the sporophytic outgrowth, without any nuclear fusion.

The sporophytic structure develops with repeated mitoses of the same sort as was described before: a leaf and a stem apex are developed from two apical cells which have appeared one after the other; a root initial is organized endogenously (*fig. 29*); scalariform vessels appear in the tissue connecting the leaf and stem origins with the root initial; and finally there is developed an independent leafy sporophyte.

From the foregoing it is clear that there is established a sporophyte with the haploid or x number of chromosomes in *Nephrodium molle*. This is the first instance yet known in plants, in which a sporophyte with the haploid number of chromosomes has been described.

Whether the sporophyte thus formed may produce spores has not yet been determined.

Discussion of cytological phenomena

APOGAMY

Since the first discovery of apogamy in *Pteris cretica*, instances of apogamy in pteridophytes have steadily increased until the phenomenon is now known in about fifty forms. No cytological studies were recorded until the appearance of the papers of STRASBURGER and of FARMER and DIGBY, already cited, but there had appeared several cytological studies of the apogamous development of the embryo in spermatophytes.

Apogamy (parthenogenesis and vegetative apogamy) is now known in spermatophytes for *Allium odorum* (TRETJAKOW **69**, HEGELMAIER **28**), Balanophora (TREUB **70**, LOTSY **39**), *Antennaria alpina*

(JUEL **30, 31**), several species of Alchemilla (MURBECK **44, 45, 46**; STRASBURGER **66**), *Thalictrum purpurascens* (OVERTON **53, 54**), *Gnetum Ula* (LOTSY **40**), several forms of Taraxacum (RAUNKIAER **57**; MURBECK **47**; JUEL **32, 33**), a number of species of Hieracium (OSTENFELD **50, 51**; MURBECK **47**; ROSENBERG **59**), and *Wikstroemia indica* (WINKLER **75, 76**). Among these contributions those of JUEL, MURBECK, OVERTON, STRASBURGER, WINKLER, and ROSENBERG present some very interesting cytological data.

JUEL (**30, 31**) made a comparative study of the parthenogenetic Antennaria and the normally fertilized *A. dioica*. In the latter a tetrad is formed from a megaspore mother cell, with the usual reduction of chromosomes, and the embryo sac is developed from one of the megaspores. There is a typical synapsis preceding a heterotypic mitosis, and the embryo sac is normal. The reduced number of chromosomes is 12–14 in the pollen mother cell and 20–24 in the integument. In the parthenogenetic *Antennaria alpina*, not only is the tetrad suppressed, but there is no trace of heterotypic and homotypic mitosis in the embryo sac. The number of chromosomes is 40–50 in the embryo sac and 45–50 in the integument. There is thus no reduction of the chromosomes during the formation of the embryo sac, and the egg retains the sporophytic number.

MURBECK (**44, 45, 46**) studied eight species of Alchemilla, chief attention being paid to the parthenogenetic *A. alpina*. In the parthenogenetic species of EUALCHEMILLA, he found that the embryo sac always developed from one megaspore of the tetrad produced from the megaspore mother cell through two successive mitoses, in which there seemed to be no evidence of a reduction of chromosomes. The number of chromosomes in these divisions is approximately 32–48, and this number is retained in the egg nucleus and the other nuclei of the embryo sac. He reports that the embryo of *A. sericata* is produced from a synergid. In the normal species *A. arvensis*, belonging to the section APHANES, he finds in the pollen mother cell 16 chromosomes—the reduced number. Two years later, MURBECK (**47**) in a short paper announced that embryos in *Taraxacum vulgare* Raunk. and *speciosum* Raunk. and *Hieracium grandidens*, *serratifrons*, and subsp. *crispatum* develop from flowers whose stamens have been removed, but he did not make any cytological studies. JUEL (**32, 33**) discovered a

peculiar development of the embryo sac in the parthenogenetic *Taraxacum officinale*. The species produced pollen with a normal reduction of chromosomes, and 13 bivalent chromosomes were present in the heterotypic mitosis; but the megaspore mother cell undergoes a single mitosis and there are formed two daughter cells, the lower one of which develops into the embryo sac. This mitosis passes through the synapsis and leptonema stages as usual, but the heterotypic figure is not organized; it is a typical vegetative one with the univalent 24–26 chromosomes. The nuclear divisions in the embryo sac were not followed by JUEL, but, accepting the results of MURBECK, he believed that the egg nucleus retained 26 chromosomes—the sporophyte number.

OVERTON (**53, 54**) found a normal reduction in the pollen mother cells of *Thalictrum purpurascens* and showed that the number of chromosomes is 24 for the sporophyte and 12 for the gametophyte. The development of the embryo sac is of two types. In some cases a tetrad is formed from a megaspore mother cell, with all the phenomena of a reduction division; the lowest cell develops into the embryo sac. But many embryo sacs are formed in a different way. The first mitotic figure in the megaspore mother cell is not heterotypic, and shows 24 univalent chromosomes; and the same number is counted in the second division in the parthenogenetic embryo. He concludes that the sporophytic number (24) remains unchanged in the embryo sac in this case, and that the egg nucleus with the sporophytic number develops into the embryo parthenogenetically.

STRASBURGER (**66**) made an extensive study of numerous species of Alchemilla § EUALCHEMILLA, the group which furnished the material for MURBECK's important discoveries. Most of the forms in EUALCHEMILLA develop normal pollen and a reduction division was found both here and in *Alchemilla arvensis* of § APHANES. In the heterotypic mitosis in the pollen mother cell, STRASBUGRER found 32 bivalent chromosomes, which MURBECK counted as 16. In the embryo sac development in apogamous species the two characteristic divisions of sporogenesis are cut out and no tetrad is formed. The nucleus of the megaspore mother cell emerges from synapsis with the sporophytic number of univalent chromosomes, and the ensuing division is typically vegetative and not heterotypic. The nuclei of the embryo sac thus contain the sporophytic number and parthenogenetic develop-

ment of the egg takes place. STRASBURGER regards the parthenogenetic tendency of EUALCHEMILLA as associated with excessive mutability, which has weakened sexuality so that the process of fertilization is being displaced by apogamy.

WINKLER (**75, 76**) reports an interesting case of apogamy in *Wikstroemia indica*. He observed that seeds are produced apogamously, in spite of the fact that some pollen matures. The apogamous development of the embryo was proved by castration experiments. He describes a peculiar phenomenon in the cells of the tapetal layer, which usually contain two to six nuclei. These nuclei fuse into a huge nucleus, whose mitotic figure often shows over 100 chromosomes; but usually he counted 52 chromosomes. Although most of the pollen does not reach maturity, a tetrad division with reduction is present in sporogenesis, and in the heterotypic figure there are 26 bivalent chromosomes. The micropyle of the ovule is closed by the elongation of the inner wall of the ovary during the formation of embryo sac, which undoubtedly may have some relation to the apogamous development of the embryo. A megaspore mother cell in this form becomes directly an embryo sac, with the entire suppression of tetrad division. His material was not sufficient for a cytological study of the mitoses, and consequently he was unable to determine the entire absence of a reduction division in the embryo sac, but it seemed very likely that the egg which develops parthenogenetically may retain the sporophytic number of chromosomes.

ROSENBERG (**59**) presents the result of cytological studies on six species of Hieracium. He took up the species of Hieracium in which apogamy was proved by the experimental studies of OSTENFELD (**52**), and traced out their nuclear details. In *Hieracium excellens* the nucleus of the pollen mother cell, after it has come out from synapsis, presents a heterotypic figure with 17 bivalent chromosomes, but often with an irregularity in the number of the bivalent and univalent ones. When daughter halves of the bivalent chromosomes separate and become grouped to form the daughter nuclei, the univalent ones are left behind in the cytoplasm, as he had already observed in Drosera (**58**). In *H. flagellare* a normal heterotypic mitosis takes place in the pollen mother cell, the reduced number of chromosomes being 21. In these two species, the embryo sac develops after a tetrad divi-

sion, as in normal cases; in rare cases the tetrad division with reduction is entirely cut out. The egg retaining the sporophytic number of chromosomes then develops the embryo parthenogenetically. But in the majority of cases he reports that while the normal development of the embryo sac is proceeding, an embryo sac from a cell quite near the tetrad (in *H. aurantiacum*), or in the integument, or in the chalazal region commences to develop. The normal embryo sac is then destroyed sooner or later by the encroaching embryo sac of vegetative origin. This development of an embryo sac from the nucellus is a new case, entirely different from those known in Funkia, Coelebogyne, Citrus, Opuntia, and *Alchemilla pastoralis*, for in the latter cases the embryo is produced directly from the nucellus, instead of through an intercalation of embryo sac formation, and hence the embryo is a vegetative bud from the sporophyte and entirely independent of gametophytic activities.

The papers of STRASBURGER and of FARMER and DIBGY, which are the latest contributions to the cytology of apogamy among pteridophytes, were briefly reviewed in the first part of this paper.

Summarizing the cytological facts in connection with apogamy among spermatophytes, as interpreted by different investigators, it seems evident that apogamy is closely associated with the suppression of sporogenesis in the megaspore mother cell. This necessarily results in no change in the chromosome number in the nucleus of the sporophytic generation, yet a structure is developed with the morphology of the gametophytic generation. Thus the embryo sac will contain the usual number of nuclei grouped in the typical manner, but these nuclei have the sporophytic number of chromosomes. From the facts of apospory, it seems probable then that the development of a gametophyte may result from an interference with the normal life-history and under conditions favorable to the gametophyte, even though the nuclei retain the sporophytic number of chromosomes.

If the doubling of chromosomes is that result of fertilization necessary to start the sporophyte generation, it is no surprise that either an egg with the sporophytic number or a vegetative nucleus with the same number may develop a sporophyte. In all the foregoing cases of apogamy this seems to be the situation.

The case of vars. *polydactyla* studied by FARMER and DIGBY is

an instance in which the apogamous development of the sporophyte is not preceded by apospory. The prothallia in these forms are produced after normal sporogenesis and consequently they contain the gametophytic number of chromosomes. The authors claim to have found in certain vegetative cells the fusion of two nuclei, one of which has entered the cell from an adjacent one, and that the sporophyte develops from the region of the prothallium where this fusion occurs. They regard this fusion of two vegetative nuclei as a substitute for normal fertilization. A similar instance of the fusion of two vegetative nuclei is given by BLACKMAN (**4**) for Phragmidium, who regards (**4**, **5**) the process as a reduced form of fertilization. The conjugated nuclei divide simultaneously through a long series of nuclear divisions, from the formation of aecidiospores to that of teleutospores, where the last pairs unite to form the single fusion nuclei within the teleutospores. There is much evidence that the period in the life-history characterized by the presence of the paired nuclei represents a sporophytic phase. Thus the fusion of the two nuclei in vars. *polydactyla* and the pairing condition of the two nuclei in Phragmidium may support as a working hypothesis the assumption that a nucleus with the sporophyte number of chromosomes is necessary for starting the sporophyte generation.

The condition shown in the apogamous Nephrodium is entirely different from anything yet recorded for plants. The prothallia are developed after normal sporogenesis and their nuclei retain the gametophytic number of chromosomes. The sporophyte then appears as a vegetative outgrowth from the prothallium, without any visible change in the nuclei, so that there is established a sporophyte with the gametophytic number of chromosomes. FARMER and DIGBY (**24**) have suggested that the number of chromosomes, approximately 60, which is found throughout the life-cycle in *Lastrea pseudo-mas* var. *cristata apospora* may be the gametophytic number in the type species, that is 72, and that this variety might have arisen from normal prothallia of the type species through apogamy. WILLIAMS (**74**) gives an instance of true apogamous development of the egg in Dictyota, which is as yet the only type among algae where the nuclear conditions of apogamy are known. In WILLIAMS' cultures the germination of the unfertilized egg with 16 chromosomes, the gameto-

phyte number, presented many irregularities in the segmentation divisions and most of the young embryos died after four divisions. Dictyota, then, cannot be regarded as furnishing an instance similar to Nephrodium, since the apogamous developments are abortive and it was not determined whether the structures were sporophytic or gametophytic in nature.

As regards the application of the terms apogamy and parthenogenesis in the various cases observed, STRASBURGER'S principle (**66**) is based upon the number of chromosomes contained in the embryo asexually produced; that is, the asexual development of an embryo from the gametophyte with the diploid number of chromosomes, no matter whether it originates from an egg or a vegetative cell, he calls apogamy; and he regards an unfertilized egg with the diploid number as a vegetative cell. He would restrict the term parthenogenesis to the asexual development of an egg, with the haploid number of chromosomes, and with the capability of being fertilized. WINKLER'S (**76**) view is different. He applies the term parthenogenesis to the case of an asexual development of an egg cell, no matter whether it be haploid or diploid, and he proposes to restrict the use of the term apogamy to cases in which the sporophyte is formed as a vegetative outgrowth from the gametophyte. FARMER and DIGBY'S (**24**) terminology, though not similar, resembles WINKLER'S. The terms euapogamy and parthenogenesis are applied respectively to cases of asexual development of the sporophyte from vegetative cells and from an egg cell of a prothallium produced aposporously; and to the case where a sporophytic outgrowth is preceded by the fusion of two vegetative nuclei they apply the term pseudo-apogamy. The apogamy in Nephrodium, therefore, would be called apogamy by WINKLER, euapogamy by FARMER and DIGBY, and represents no category given by STRASBURGER.

ALTERNATION OF GENERATIONS

Since HOFMEISTER'S investigations we have known that the life-history of most plants involves a regular alternation of sexual and asexual generations. The subject has been discussed by many authors, such as CELAKOWSKY (**13, 14, 15**), SACHS (**60**), BRAUN (**10**), PRINGSHEIM (**55, 56**), VINES (**72**), DE BARY (**2**), BOWER

(7, 8, 9), VAIZEY (71), STRASBURGER (65, 67), BEARD (3), CAMPBELL (11, 12), SCOTT (61), LANG (36, 37), KLEBS (34, 35), HARTOG (27), COULTER (18), DAVIS (19, 20), WILLIAMS (73), BLACKMAN (4, 5), WOLFE (77), LOTSY (41, 42), GRÉGOIRE (25), CHAMBERLAIN (16), CHRISTMAN (17), OLTMANNS (49), HARPER (26), YAMANOUCHI (80), and many others.

Among thallophytes no generalization for the whole group is possible at present, partly because of extreme diversity, and partly on account of the meagerness of our knowledge regarding the life-cycle of the majority of the forms. Different opinions are held concerning the nature of the phenomena in various forms, and some even question the existence of an alternation of generations. However, it is now being gradually established by actual investigation, and quite recently cytological proof has been obtained from several forms, as Dictyota, Phragmidium, Nemalion, Polysiphonia, and some others.

Pteridophytes and bryophytes have been regarded as the best illustrations. Discussion in connection with the pteridophytes has not been in reference to the existence of alternation, but has centered about the question whether it is to be interpreted as of antithetic or homologous origin.

These two views represent different conceptions as to the origin of the sporophyte. Those who advocate the theory of antithetic origin regard the sporophyte of pteridophytes as a gradual elaboration from the zygote of some aquatic algal ancestor, a new phase having thus been intercalated in the life-history. This view was first clearly stated by CELAKOWSKY (13, 14). BOWER (7, 8, 9) supported it and endeavored to explain it as an adaptation to external conditions. STRASBURGER (65), restating the position in terms about identical with BOWER'S, based the theory upon nuclear details. Those who maintain the theory of homologous origin consider that the sporophyte arose as a modification of the gametophyte, and not as a new structure. PRINGSHEIM (55, 56), and more recently SCOTT (61), LANG (36, 37), COULTER (18), and others advocate the homologous theory. This theory is largely based upon the phenomena of apogamy and apospory and also to a certain extent upon experiments in regeneration.

When these two theories were proposed, cytological investigations had not yet developed, and even LANG'S admirable work did not

touch any cytological particulars. Since the announcement of STRASBURGER'S view of the antithetic origin of alternation, the first to be based on cytological details, chief attention has been directed by many workers to the behavior of chromosomes during the reduction division in the normal life-cycle. As to the results of such accumulated studies, the various views are not readily grouped. However, the majority of cases confirms the view that the periodic reduction of chromosomes is necessary; in other words, the gametophyte with the x number of chromosomes is entirely distinct from the sporophyte with the $2x$ number, and the transition from one generation to the other is marked by the reduction of chromosomes in sporogenesis and the doubling of chromosomes in fertilization, in connection with which the predominant characteristics of one generation are entirely lost and the potentialities of forming the other generation are regained.

As stated above, the cytological work on apogamy and apospory has been chiefly among flowering plants; and quite recently our knowledge concerning these phenomena in ferns was extended by the contribution of FARMER and DIGBY (**24**) on Lastrea, Athyrium, and Scolopendrium, and of STRASBURGER (**68**) on Marsilia. According to these investigations, apogamy, whatever its cause may be, is always preceded either by apospory or the fusion of two vegetative nuclei, which seems to favor the view that the $2x$ number of chromosomes is necessary to establish the sporophyte. Apogamy and apospory, which have been the chief argument for the theory of homologous origin, now seem to support the theory of antithetic origin.

As a matter of fact, the nuclear condition in Nephrodium in the normal life-cycle confirms the antithetic theory; but apogamy in Nephrodium introduces a new situation. In this case apogamy is preceded neither by apospory nor fusion of vegetative nuclei, but the sporophytes are developed with the haploid number of chromosomes. If it might be questioned whether the situation in Nephrodium—in which the nucleus of the gametophyte with the x number can establish the sporophyte—may favor the idea of homologous origin, it must be remembered that we have such abnormal cases of apogamy and apospory in flowering plants, where the embryo sac (probably gametophytic) does not contain the characteristic x number of chromosomes, but always the $2x$ number.

Conclusion

According to the present interpretation of the value of chromosomes, in *Nephrodium molle* Desv. there is present an antithetic alternation of generations marked by the number of chromosomes.

Apogamy in Nephrodium presents a new situation, where the sporophyte is developed with the haploid number of chromosomes. This seems to be an abnormal case, but it must be admitted that it shows that the number of chromosomes is not the only factor which determines the characters of the sporophyte and gametophyte.

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NOTE.—After this paper was in type, STRASBURGER's "Chromosomenzahlen, Plasmastrukturen, Vererbungsträger und Reduktionsteilung" (Jahrb. Wiss. Bot. **45**:479–568. *pls. 1–3.* 1908) appeared. It not only presents results of investigations on *Lilium Martagon* dealing with the chromosome situation during embryo sac formation and pollen tube development, but it also contains voluminous data concerning plasma structure, chromosomes as bearers of hereditary characters, and the phenomena of the reduction division, the discussion being based upon works of various invesitgators of both plant and animal cells.

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EXPLANATION OF PLATES IX AND X

The figures were drawn with the aid of an Abbé camera lucida, under Zeiss apochromatic obj. 1.5^{mm} N. A. 1.30, combined with compensating ocular 18; except *figs. 9, 10, 11, 12, 13, 14, 20, 21, 28a* drawn with compensating ocular 4; and *figs. 28, 26*, and text cuts drawn under combination of dry obj. 4^{mm} and ocular 4. The plates and text cuts are reduced to one-half the original size.

FIGS. 1–3 are in the text.

PLATE IX

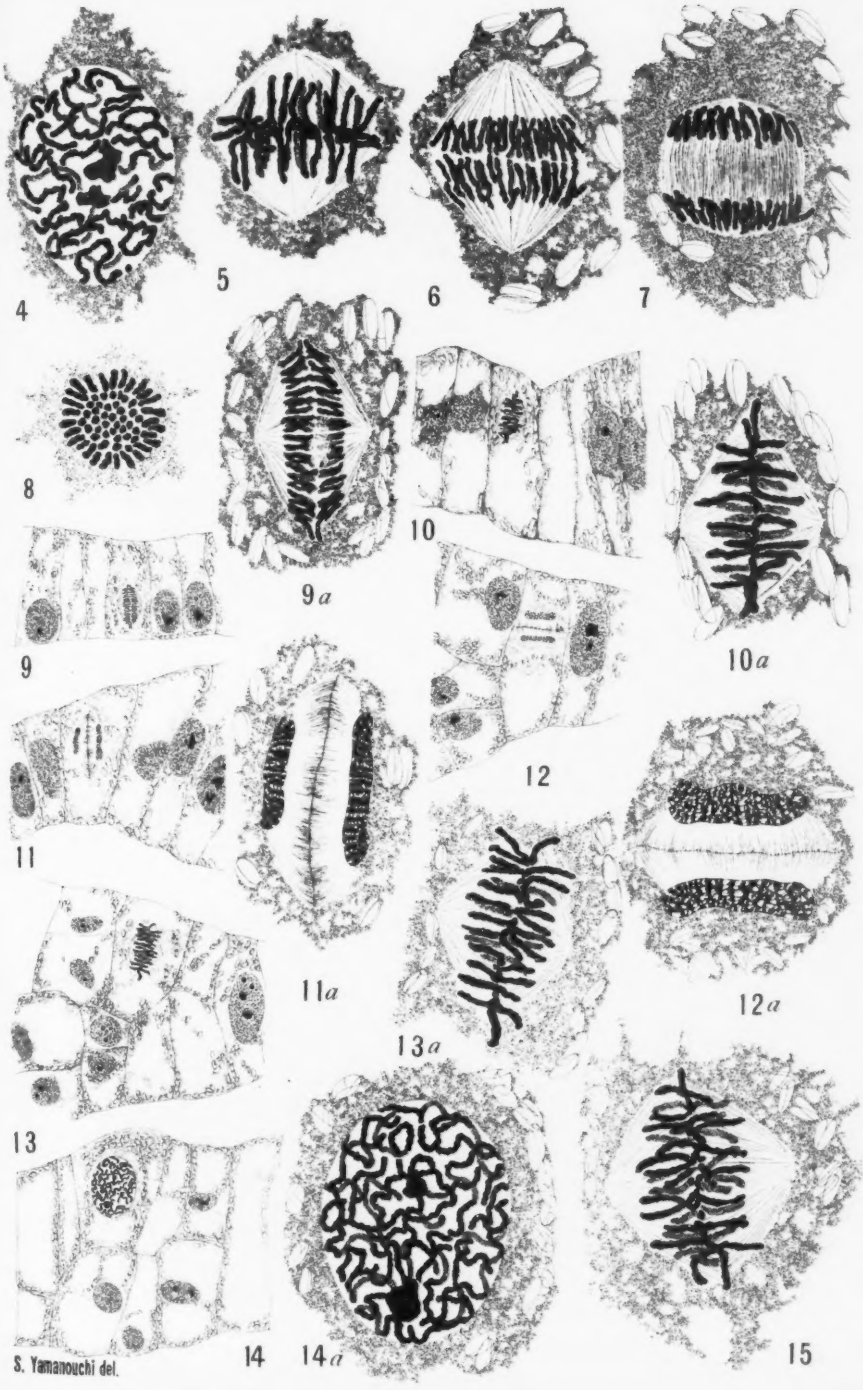
FIG. 4.—Nucleus of vegetative cell of an apogamous prothallium; spirem formed; two nucleoli present.

FIG. 5.—Late prophase; long slender chromosomes present, previous to their arrangement in an equatorial plate.

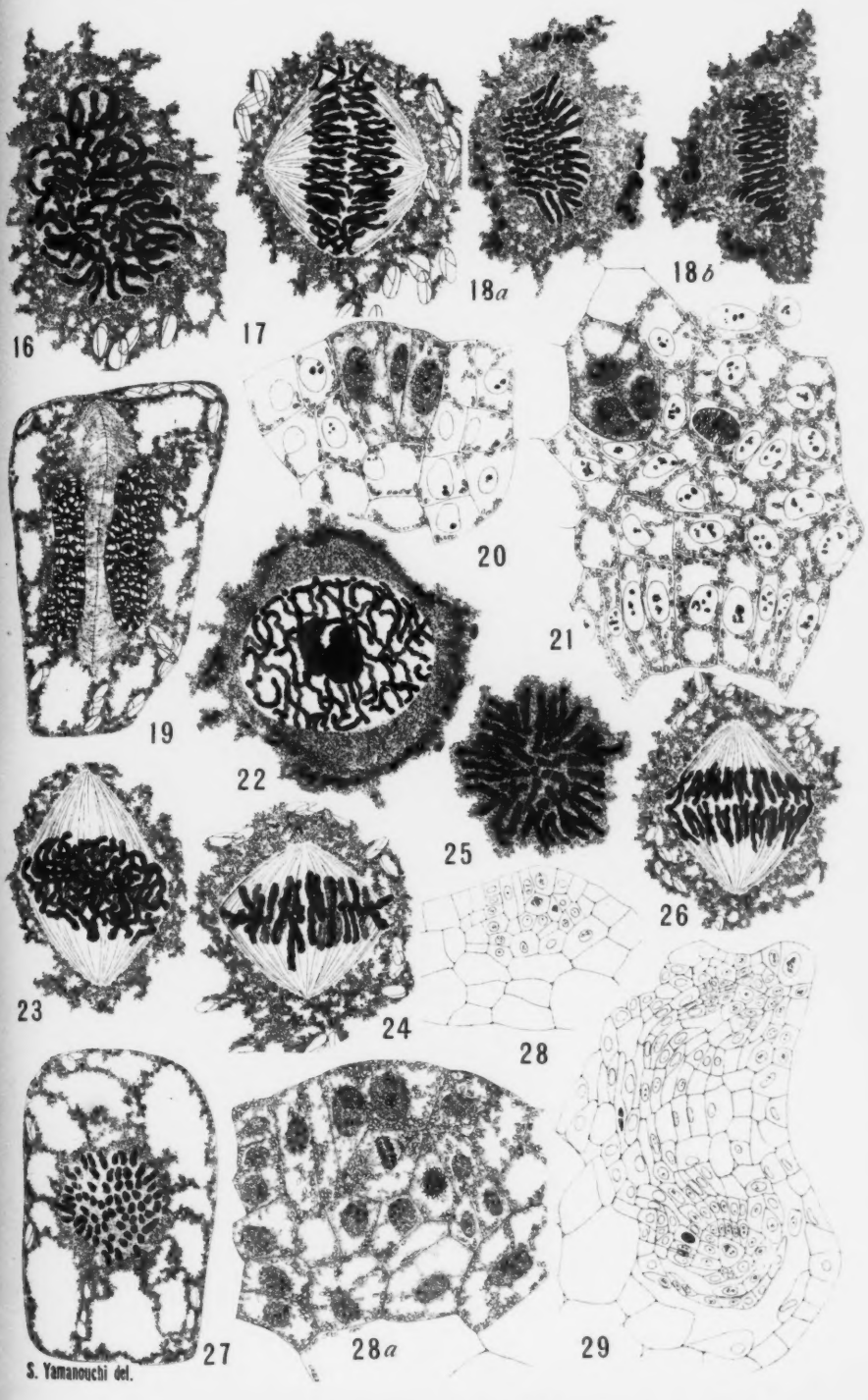
FIG. 6.—Metaphase; two daughter halves of each chromosome just separated.

FIG. 7.—Late anaphase; daughter chromosomes grouped at two poles.

FIG. 8.—Polar view of late anaphase; 64 chromosomes present in a group.



YAMANOUCHI on NEPHRODIUM



YAMANOUCHI on NEPHRODIUM

FIG. 9.—Section through region where later a cushion arises; narrow cells parallel.

FIG. 9*a*.—Nucleus in metaphase from previous figure, under higher magnification.

FIG. 10.—Section through region forming cushion; next stage after that shown in *fig. 9*.

FIG. 10*a*.—Nucleus in late prophase from previous figure, under higher magnification.

FIG. 11.—Section through region forming cushion; later stage than that shown in *fig. 10*.

FIG. 11*a*.—Telophase of nucleus shown in previous figure, under higher magnification.

FIG. 12.—Section including cushion region; next stage after that given in *fig. 11*.

FIG. 12*a*.—Mitotic figure in telophase, shown in *fig. 12*, under higher magnification; cell plate laid down parallel to surface of prothallium.

FIG. 13.—Section of cushion region; a nucleus within superficial cell in metaphase.

FIG. 13*a*.—Nucleus in metaphase, shown in the previous figure, under higher magnification.

Mitosis in conspicuous superficial cell

FIG. 14.—One of the sections of the cushion region shown in *fig. 3* (text); one superficial cell has increased considerably in size; nucleus in prophase.

FIG. 14*a*.—Nucleus in prophase, shown in *fig. 14*, under higher magnification; several ends of the spirem seen are cut sections; two nucleoli present.

FIG. 15.—Late prophase, showing long slender chromosomes before arrangement in an equatorial plate.

PLATE X

FIG. 16.—Polar view of the late prophase shown in preceding figure.

FIG. 17.—Metaphase; two daughter halves of each chromosome just separated.

FIGS. 18*a*, 18*b*.—Two groups of daughter chromosomes in late metaphase of a nucleus cut obliquely into two sections; 66 chromosomes present.

FIG. 19.—Telophase; cell plate, vertical to surface of prothallium, laid down to cut superficial cell into two daughter cells.

FIG. 20.—Portion of section cut through cushion region; three superficial cells drawn showing contents, middle one of which is cut obliquely as an apical cell.

FIG. 21.—Surface view of a stage similar to that shown in preceding figure; the three superficial cells in question represented by drawing all the contents.

Mitosis in interior cells directly beneath superficial cells

FIG. 22.—Nucleus containing a spirem; visible ends of spirem are cut sections.

FIG. 23.—Prophase; chromosomes irregularly crowded in a mass.

FIG. 24.—Late prophase, showing chromosomes before their arrangement in an equatorial plate.

FIG. 25.—Polar view of metaphase, where L-shaped chromosomes are arranged in an equatorial plate; vertical arms of L's are visible as dots and lateral arms as radiating lines.

FIG. 26.—Late metaphase; two daughter halves of each chromosome have just separated.

FIG. 27.—Early telophase, showing polar view of a group of daughter chromosomes; 66 chromosomes present.

FIG. 28.—Section of cushion region where a sporophytic structure has been worked out.

FIG. 28*a*.—Approximate portion that belongs to the sporophytic structure shown in the preceding figure, under higher magnification; difference of size of cells in prothallial region and sporophytic structure shown.

FIG. 29.—Section through sporophyte apogamously produced, in a considerably later stage; one of the two apical cells seen is a leaf initial, the other a root initial; apical cell of stem not drawn in this section; no structure standing for a foot is present.

ALPINE VEGETATION IN THE VICINITY OF LONG'S PEAK, COLORADO

WILLIAM S. COOPER

(WITH EIGHT FIGURES)

This paper is the result of observations made during the summers of 1904 and 1906. It makes no pretensions to completeness, but is intended to serve as a general survey of an intensely interesting region. It is the intention of the author immediately to begin a more extensive and detailed study.

My thanks are due, first of all, to Dr. E. N. TRANSEAU of the Charleston (Ill.) Normal School, and to Dr. D. S. JOHNSON and Dr. CHARLES K. SWARTZ, of Johns Hopkins University, for many valuable suggestions; also to Dr. AVEN NELSON, of the University of Wyoming, for determination of plants.

I. Location and general topography

The Front Range of the Rocky Mountains, which in the vicinity of Long's Peak constitutes the continental divide, is a rugged mass carved from the Archean granite and gneiss. South of Long's Peak, which is an eastern projecting spur therefrom, its direction is nearly north and south, and it stands about 24^{km} west of the eastern border of the mountain region. North of Long's Peak it turns to the northwest, and continues in this direction for a distance of 24^{km}, until it meets the Medicine Bow and Rabbit Ear Ranges; the continental divide is continued in the latter range. At the eastern base of the Front Range, just north of Long's Peak, lies Estes Park, a mountain valley which here separates the main range from the lower forest-clad mountains toward the east. Estes Park lies at an altitude of 2285^{m}; the average altitude of the divide is 3810^{m}; most of the peaks exceed 3900^{m}, and Long's Peak attains an altitude of 4350^{m}.

The localities studied are on the summit and eastern flank of the Front Range, from Mt. Tyndall, 6.4^{km} south of Long's Peak, to Stone's Peak, 16^{km} northwest. Particular attention was given to two glacial cañons: the Chasm Lake cañon, immediately below the east face of Long's Peak; and Glacier Gorge, west of the same mountain.

II. Physiography

A. PRESENT.—For convenience we may divide the physiographic features of the region into two groups: (1) the flat summit of the divide and slopes similar to it; (2) the glacial cañons.

The summit of the divide is an elevated plateau, in some portions level, more often gently rolling (*figs. 1, 2*). In places it is 1.6^{km} or more wide, in others it narrows to less than 0.4^{km}. A few low peaks rise from it, often near its edge, so that they have a precipitous face on that side. The surface is covered with a rather thin layer of rock

FIG. 1.—Summit of the continental divide from Stone's Peak; Long's Peak at the left; the dry meadow covering the flat surface of the divide is shown.

fragments split off by frost and temperature changes, of small size in most places, but much larger on the higher summits. Similar in every way to the summit of the divide are the slopes that descend to the region of timberline where glacial erosion has not formed cliffs.

The glacial cañons head in a series of fine cirques, immediately under the steep cliffs that form the face of the continental divide (*fig. 3*). They are separated from each other by projecting spurs of varying width, sometimes flat-topped, but oftener mere ridges, so close together were the sources of the glaciers. When flat-topped they are essentially similar to the summit of the divide, and are in fact continuous

with it, being covered with a thin layer of frost-broken fragments. Some of the ridges bear high rugged peaks, but in most cases they decrease gradually in altitude away from the divide, and frequently end in long interlobate or medial moraines, where the adjacent glacier tongues met or coalesced. The floors of the cañons descend toward the lower altitudes in an alternating series of very gentle slopes and abrupt steps, the latter often 30^{m} or more in height.

B. HISTORICAL.—A glance at the physiographic history of the region will make clearer the present conditions and processes. For

FIG. 2.—Summit of the divide near Mt. Tyndall; a more detailed view of the dry meadow, showing also the top of cliffs that surround a glacial cirque.

the purpose of this paper, it is unnecessary to go back farther than the time of Pleistocene glaciation, since during that period practically every trace of vegetation must have been destroyed. The Front Range in the region studied was glaciated during the Pleistocene period over a width of about 25^{km1}. The summit of the range was deeply covered with snow, which, accumulating in larger quantities in favorable locations along the flanks of the range, became consolidated at these points into glacier ice and commenced the work of shaping and modifying the cañons.

[1] KING, CLARENCE, Exploration of the Fortieth Parallel.

In due time the climate began to change and the amount of snow to decrease accordingly. Finally, the winter snowfall decreased to such an extent that the summit of the divide and the gentler slopes became bare during the summers. These surfaces had heretofore been protected by their load of snow from the process of weathering. Now, however, began the work of frost and of temperature changes, which is responsible for the condition of the summit today. The thinness of the covering of rock fragments on these surfaces is due to the protection from sudden changes of temperature afforded the solid rock beneath by the broken rock itself, with the layer of vegetation that has become established upon it.

FIG. 3.—View in Glacier Gorge, showing glacial topography and wet meadow areas on ledges; a glacial lake in the foreground, and snow banks below the cliffs.

In the meantime the glaciers themselves steadily shrank, because of the decreasing supply of snow at their sources. The large accumulation of névé in the cirques, however, enabled them to hold out long after the perennial snow mantle of the summit and exposed slopes had disappeared. In fact, there still remain at the heads of several of the cañons remnants of the former ice tongues, which, though small, are true glaciers.

The cañons thus formed exhibit the usual glacial characteristics

(*figs. 3–6*). At their lower ends are found series of terminal moraines and for some distance up there are extensive lateral moraines. The floors of the cañons, except for an occasional small terminal moraine, are nearly bare of morainic material, such as is present being an exceedingly sparse scattering of single bowlders. The floors are very smooth, frequently almost polished, and are marked by the usual scratches and striae. *Roches moutonnées* are numerous but not prominent. At intervals are found the great "steps" mentioned above, where were the ice falls of the glaciers. At their bases are

FIG. 4.—Smooth glaciated floor of Glacier Gorge, with scattered glacial detritus; the wet meadow patches have formed among this material.

nearly always lakelets, occupying basins excavated by the ice, which naturally possessed increased erosional power at these points. Lake basins are not, however, exclusively confined to the bases of the "steps."

The results of post-glacial weathering in the cañons are seen in the masses of talus piled along the bases of the cliffs. Where the cañons are narrow, the weathered material covers the whole breadth of the floor, and has begun to fill many of the lake basins with large fragments. Usually, however, there is a wide central space which the talus from the side cliffs does not reach. Another effect of weather-

ing, more important ecologically than physiographically, is the enlarging of the cracks or joint planes in the smooth floor of the cañons, by disintegration of their edges and the deposit, in or near the cracks, of the fine disintegrated material. Stream erosion has so far produced practically no effect upon the topography of the upper portions of the cañons.

III. Vegetation

In considering the vegetation of the higher mountain region, we naturally divide it into two great formations: the alpine grassland, and the forest, and place the division between these at timberline. In general this arrangement is a right one for the region, but in studying the vegetation dynamically we are compelled to recognize an exception in the wet meadows of the cañons. Above timberline we find two types of grassland: the dry meadow, occupying the exposed slopes and ridges; and the wet meadow, in the upper portions of the glacial cañons. The former is a true climatic grassland. The latter, however, as will be shown, is probably not permanent grassland brought about by climatic factors, but is a stage in the forest succession, and, conditions remaining the same, will become forest after the lapse of sufficient time. In this paper the term "alpine grassland" will be used to include both dry and wet meadow. We will consider first the development of these two types of alpine meadow; and second, the forest formation in its successional relation to them.

A. THE ALPINE GRASSLAND

1. *The dry meadow*

The societies which form the stages in this succession (*figs. 1, 2*) cover a large part of the area above timberline—an area which is practically coextensive with the flat summit of the range and the slopes similar to it, which, as has been said, are covered with a layer of broken fragments. While this layer of broken material protects the bed rock from further weathering, the fragments themselves are continually disintegrating under the influence of frost and of lichens. Disintegration by lichens is an important process here as is evidenced by the thick crust of these plants upon every stone.

Every stage in the development of the dry meadow may be seen on the summit of the range. On the more elevated portions, where

have been split off blocks of very large size, no plants except lichens have as yet been able to gain a foothold. Where the blocks are smaller and more disintegrated, a layer of fine material has accumulated around and among them—the first step in the formation of a soil; and here a few herbaceous plants of extreme xerophytic nature, such as *Silene acaulis*, *Phlox caespitosa*, *Dryas octopetala*, have established themselves. A further stage is seen where the vegetation has become more luxuriant both in number of species and of individuals, frequently partially concealing the remnants of the disintegrating rock fragments. In the mature dry meadow the rock fragments have mostly broken down to form, with the humus deposit, an even layer of soil which is well covered by a growth of low herbaceous vegetation. The dry meadow of this region resembles quite closely the so-called "alpine tundra" of the summit of Mt. Ktaadn, Maine, as described by HARVEY,[2] and observed by the author of this paper. It differs from that in the practical absence of mosses and fruticose lichens so characteristic of the summit of Ktaadn. At the same time, it does not perfectly correspond with the common idea of meadow land, since the vegetation is low and of a decidedly xerophytic nature. As is the case in the Pike's Peak region[3] the mature dry meadow has two seasonal stages, the earlier characterized by the prominence of *Rydbergia grandiflora* in flower, the later by *Campanula rotundifolia*. It must not be supposed that the soil on these exposed summits and slopes, thin as it is, is everywhere dry. Even along the summit of the divide are frequent depressions receiving all the run-off from the surrounding slopes, which often are gentle and embrace large areas. The solid granite beneath prevents absorption; therefore the water remains stagnant or flows very slowly over the surface. The supply seems to be fully equal to the loss by evaporation, for these areas remain wet all summer long. The depressions are characterized by a more luxuriant vegetation, and therefore deeper deposits of humus, but the species are the same as those found on the drier portions of the meadow. A list of the dominant species of the dry meadow follows:

[2] HARVEY, LEROY H., A study of the physiographic ecology of Mt. Ktaadn, Maine. University of Maine studies, No. 5.

[3] CLEMENTS, F. E., Research methods in ecology.

PRINCIPAL SPECIES.—Silene acaulis L., Sieversia turbinata (Rydb.) Greene, Dryas octopetala L., Phlox caespitosa Nutt., Campanula rotundifolia L., Rydbergia grandiflora (T. & G.) Greene.

SECONDARY SPECIES.—Selaginella densa Rydb., Deschampsia caespitosa alpina Vasey, Trisetum subspicatum (L.) Beauv., Carex atrata L., Juncoides spicatum (L.) Kuntze, Zygadenus coloradensis Rydb., Lloydia serotina Reichenb., Polygonum viviparum L., Oreobroma Grayi (Britton) Rydb., O. pygmaea (Wats.) Howell, Arenaria sajanensis Willd., Draba crassifolia Graham, Sibbaldia procumbens L., Dasiphora fruticosa (L.) Rydb., Trifolium dasyphyllum T. & G., Oreoxis alpina (Gray) C. & R., Primula angustifolia Torr., Androsace subumbellata (A. Nels.) Small, Douglasia Johnstonii A. Nels., Polemonium confertum Gray, Mertensia viridis Nels., Castilleja puberula Rydb., Pedicularis Parryi Gray, Solidago scopulorum (Gray) A. Nels., Tetraneuris acaulis (Nutt.) Greene, Tonestus pygmaeus (T. & G.) Nels., Erigeron pinnatisectus (Gray) Nels., Artemisia scopulorum Gray.

2. *The wet meadow*

It must be borne in mind that on account of a smaller deposit of snow, due to exposure to the wind and sun, the summit of the range and the unglaciated slopes were first exposed, while the cañons still contained glaciers fed from the névé accumulated in the cirques at their upper ends. Thus it was long after the dry meadows above had begun their development when vegetation, following the retreat of the ice, first gained access to the upper portions of the cañons. At the present day the spruce-fir forest extends up the cañons to an altitude of about 3350^{m}. Above this is an area supporting a mesophytic meadow vegetation, which, however, only partially covers the ground, being confined to the vicinity of the watercourses. Still higher, where the last remnants of the ice lingered, there is no vegetation save a sparse growth of lichens. In the heads of the cañons, therefore, we may study primary invasion in all its stages, and the next few paragraphs will be devoted to a description of it as observed in these places.

A. THE GLACIAL CAÑON AS A HABITAT.—*Atmospheric conditions.*—As to the atmospheric conditions in the cañons I can give no exact data, but it may be said with certainty that they are comparatively favorable to plant growth—much more so than in the region of the dry meadows. The most noticeable difference between the two habitats, in regard to atmospheric conditions, is the exposure to the full force of the wind on the dry meadows, contrasted with the effective shelter

from that agent afforded by the cañon walls. The difference in altitude between the two habitats, averaging about 610^{m}, also favors the cañons, since atmospheric rarity tends to increase evaporation.

Ground water.—The smooth polished floor of the cañons has already been described. In some parts the surface slopes gently and evenly; in others there are low rounded prominences (*roches moutonnées*) with depressions between. The greater part of this region is dry during all of the growing season, since the surface drainage from the snow banks above is the only source of moisture that need be taken into account. The small amount of rainfall during the growing season may be neglected altogether, since the smooth rock surfaces cannot retain it, and it very soon evaporates or joins the drainage channels from the snows. Snow accumulates at the bases of the upper cliffs in large quantities, and many of the drifts remain through the summer, affording by their melting a constant supply of water to a restricted portion of the area below. The drainage channels from the various permanent drifts form a network over the cañon floor in following the principal depressions among the *roches moutonnées*. Some cases were observed where the water flowed in a broad sheet for long distances over a smooth gently sloping rock surface.

Sources of soil materials.—The soil materials which render possible the establishment of the pioneers of the higher plants are derived principally from two sources: rock decay and wind-blown dust. Rock decay has made very little progress in the cañon heads since glacial times. Since the process is conditioned by the presence of moisture, the larger part of that which has been done and is now being done is within the sphere of influence of the drainage channels. As has been said in describing the physiography of the region, decomposition is going on principally along joint planes, and the fine products of this process are either deposited in the cracks near to where they were produced or are carried down by flowing water and deposited in other situations.

I believe that wind-blown dust is an important addition to the scanty supply of soil material available to the pioneers. Its source doubtless is largely the dry meadows above the cañons, where during the summer large areas of sparsely covered soil become desiccated. Some of the dust from this and other sources is doubtless carried

directly to its final destination on the cañon floors. It is likely, however, that a greater amount is brought down by the streams from the snow banks at the base of the upper cliffs, upon which it had fallen, perhaps years before. The wet surface of the drifts would hold all such fine material deposited upon it. This deposit is not so slight as might be imagined, for during a single summer the drifts become so coated with dust that the discoloration is conspicuous at a great distance. The fate of the dust thus deposited is as follows: Most of the run-off from a large snow bank in an arid mountain region comes from the melting of the compact basal portion. The water which results from surface melting nearly all evaporates. Thus the layer of dirty snow upon the surface of the drift is slowly but continually sinking. Each winter a fresh layer of snow is deposited, which, during the following summer, accumulates a layer of dust upon its surface. Frequently a section through a snow bank will reveal a series of these dirt bands, roughly marking off what remains of each winter's snowfall. It is evident that because of the basal melting, these dirt bands will finally sink to the bottom of the drift, and that the matter which the dirty layers contain will be carried down with the stream of water which issues from beneath the snow bank, often with great velocity. This material, converging from numerous sources to a few restricted drainage areas, is by no means to be neglected, and being chiefly organic in nature, it is a valuable contribution to the making of the first soil. Being exceedingly fine material, it may be carried to a considerable distance, and is deposited in basins, or wherever the velocity of the stream slackens. The disintegrated rock material, on the other hand, being comparatively coarse, if carried away at all, is deposited very near to its point of origin.

As soil producers, lichens have accomplished practically nothing in the glacial cañons. The fact that the rock is a hard granite, and the smoothness of its surface, as well as the comparatively short time that the rock has been exposed, are sufficient to explain this.

B. THE INVASION OF THE CAÑONS.—The unimportance of lichens in preparing for the establishment of the higher plants has just been mentioned. The advance of the latter must therefore be conditioned by the other sources of soil material, rather than by any furnished by lichens. And so we find two groups of invaders, one making use

principally of the decomposed rock material in the cracks, the other developing later, but usually on new ground, in basins and very wet places, and profiting from the organic material brought down from the snowdrifts.

In cracks and joints of the floor we find a pioneer group consisting of the following species, all but one or two of which are perennials.

1.—Deschampsia alpicola Rydb., Agrostis tenuiculmis Nash, Trisetum subspicatum (L.) Beauv., Carex atrata L., Juncoides spicatum (L.) Kuntze, Sagina Linnaei Presl., Draba crassifolia Graham, Sibbaldia procumbens L., Androsace subumbellata (A. Nels.) Small, Artemisia scopulorum Gray.

2.—Salix petrophila Rydb., Oxyria digyna (L.) Camptd., Saxifraga debilis Engelm., Senecio Fremontii T. & G.

The species in the first group, to which further exploration would doubtless add many more, are commonly found in the dry meadows. Since these meadows are all above the level of the cañon floors, this group of pioneers must have come from seeds blown or washed down from them. There is one other possibility—that these plants have followed the glaciers as they retreated. It seems likely, however, that pioneers in the invasion of the lower portions of the cañons were plants belonging to lower altitudes and more favorable conditions; since they were as well sheltered from the wind as are the pioneers of today, and the water supply was far more abundant. The plants in the second group are commonly found in clefts and among bare talus in the higher altitudes. These species, with those of the first list, constitute a group of invaders of xerophytic character from higher altitudes. They do not occupy a definite zone, but are scattered over a broad area of the cañon floor wherever conditions permit them to exist. In some measure they prepare the way for the group of invaders that comes from the opposite direction, but like the lichens they are relatively unimportant, and, as will be shown, the plants that come in from below to fill the depressions may be entirely independent of any aid from earlier arrivals. Sometimes, however, the cracks containing these plants may become the starting-point for quite large mats of turf. If the water supply is abundant enough to make possible the establishment in a crack of the more mesophytic sedges and grasses, such as grow in the basins soon to be described, these may spread out over the surface of the rock by means of rootstocks, form-

ing a thick and permanent carpet which may be lifted from the rock at its edges, but which is firmly anchored at its point of origin.

We now come to the group of invaders that is advancing toward the heads of the cañons from below. The pioneers are few in species, but exceedingly numerous in individuals, covering the areas over which they advance with a thick carpet of vegetation. Their line of attack is along the watercourses. It has been said that deposition of earthy matter from the melting snows, fine rock material, and some organic matter from the plants growing in cracks farther up, is continually going on where the current of the watercourses slackens. The first plants to appear in this sediment are usually mosses, including *Philonotis fontana*, which sometimes becomes established even in shallow water. The mosses are followed by species of Carex, which by means of their creeping stems spread extensively and form thick mats. Grasses now come in, with a scattering of other herbs characteristic of marshy ground and stream banks, nearly all of which are found in marshy situations at considerably lower altitudes. The deposits of humus from these plants hastens the filling-in of the depressions, and the result is a wet swampy meadow with one or

FIG. 5.—View in Chasm Lake Cañon; the wet meadow vegetation in the foreground has completely filled a basin; similar patches of vegetation are visible in the vicinity of the cascades.

more streams meandering through it (*fig. 5*). These streams often run over the rock itself, since the current has so far kept their beds free from sediment. Prominent plants growing in these wet meadows are as follows:

Lycopodium selago L., L. annotinum L., Carex (several species) dominant, Caltha rotundifolia (Huth) Greene, Sedum rhodanthum A. Gray, Sieversia turbinata (Rydb.) Greene, Kalmia microphylla (Hook.) Heller, Primula Parryi A. Gray, Gentiana frigida Haenke, G. plebeja Holmii Wettst., Swertia congesta A. Nels., Elephantella groenlandica (Retz.) Rydb., Crepis alpicola (Rydb.) A. Nels.

Later a few shrubs make their appearance. *Betula glandulosa* is by far the commonest of these, and *Dasiphora fruticosa* and *Salix chlorophylla* are frequent.

Where a stream flows among glacial débris scattered over a smooth gently sloping rock surface, plants themselves are instrumental in forming small basins. Fine material accumulates around the rock fragments, and in this mosses obtain a foothold. From the rock fragments as centers mats of moss spread out, and these coalescing partially dam up the stream, so that more fine material is deposited. The development of the meadow then progresses as in the natural rock basins. Frequently the damming-up of its course deflects a portion or all of the stream, and in its new course it encounters other débris where the process is repeated. These little meadow patches often coalesce to form areas of quite respectable size. The turf mats that start from the cracks also sometimes become joined to these, and thus in various ways considerable areas on the cañon floors obtain a solid covering of herbaceous vegetation (*figs. 4, 6*). Ledges on the cañon walls, where water trickles over them, are covered with a turf mat similar in composition to that upon the cañon floor (*fig. 3*). Where cascades occur, principally at the great "steps," there is naturally an abundant vegetation, consisting of mosses, sedges, and other herbs growing within the influence of the spray (*fig. 5*). The lake basins are so large and deep that comparatively little filling has been accomplished. The shallower portions along the shore are partially converted to meadow, and where a lake occurs at the base of a "step" good-sized alluvial cones extend out into the water at the upper ends. Of course this is not the case with the highest lakes, where very little alluvial matter is available.

The mature wet meadow is thus of a decidedly mesophytic character. Composed as it is of a thick bright-green turf of sedges, grasses, and other flowering plants, it has a truly meadow-like appearance.

It must be borne in mind that only the depressions have been thoroughly taken possession of by vegetation (*fig. 6*). The higher and drier portions of the cañon floor—the *roches moutonnées*—including much more than half of the total area, are still bare, save for a sparse covering of lichens, and a few xerophytic herbs in the crevices. These areas, of course gradually decreasing, but with

FIG. 6.—View looking down Glacier Gorge; the dark areas in the foreground are wet meadow occupying depressions in the cañon floor; scattered over the meadow areas are still darker patches, the Picea *Krummholz;* farther down the cañon may be seen the Picea-Abies forest surrounding two glacial lakes.

exceeding slowness, are destined to remain very much the same for a long time. Far down the cañons, in the midst of the forest, there are many places where the bare floor is still exposed, more incrusted with lichens and slightly more decomposed, but nevertheless surprisingly similar to the bare areas at the cañon heads.

B. THE FOREST

For the present purpose we need to consider only the upper forest zone, which in this region is composed of two societies governed by

the factor of soil water content. The white pine society consists of an almost pure growth of *Pinus flexilis*. It covers the dry summits and upper slopes of the ridges between the cañons up to the limit of tree growth. The spruce-fir society is confined to situations where there is an abundant soil water content. It follows the cañon bottoms up to where they emerge above timberline, and extends up the sides as far as there is a sufficient amount of ground water available. The two trees that dominate the society are the Engelmann spruce (*Picea Engelmanni*) and the subalpine fir (*Abies lasiocarpa*). The latter is more abundant close to the streams, and seldom or never in this region ascends quite to timberline.

1. *The Krummholz* (*figs. 7, 8*)

The altitude of the present upper limit of tree growth averages about 3350^{m}, with a range between extremes of perhaps 150 or 180^{m}. Since *Abies lasiocarpa* does not ascend to timberline, the *Krummholz* is composed of two trees only, *Pinus flexilis* and *Picea Engelmanni*, the former on the ridges, the latter in the cañons. Both reach their upper limit at approximately the same altitude, but their appearance and behavior there is so strikingly different that a description of each will be of interest.

PINUS FLEXILIS.—This tree, even when growing in its most congenial habitat, is very irregular and contorted. In its *Krummholz* form it assumes the most fantastic shapes and yet in all of these a general uniformity of behavior may be seen. A very typical growth of the *Krummholz* form is found at timberline on the Long's Peak trail (*figs. 7, 8*). Here there is considerable exposure to the prevalent west wind which sweeps with great force over a saddle on the ridge behind. The trees form an open growth, with the individuals usually growing singly. They are of great age, and often 30^{cm} thick, but few are more than 1.5^{m} in height. The live branches all point to the eastward, those on the windward sides are dry and dead, and the windward portions of the trunks are in nearly every case devoid of bark. Frequently the greater part of the trunk is worn away by the ice particles borne by the winter gales. The degree of exposure to the winds from the west determines the height of the tree. If somewhat sheltered, the trunk may be nearly erect, but in the most exposed places it becomes

absolutely prostrate (*fig. 8*), creeping along the ground for 4.5 to 6^{m}, and sometimes partially or wholly buried in sand and needles. It is a noticeable fact that on the ridges the *Krummholz* ends abruptly—in other words there is a very definite timberline. Beyond the main mass of the forest outlying groups of trees are rare, and are never at any distance from it.

PICEA ENGELMANNI.—In the cañons, on the contrary, it is seldom possible to determine the precise limit of the forest formation. In ascending we find that the trees become more scattered and at the same

FIG. 7.—*Krummholz* form of *Pinus flexilis* near the Long's Peak trail; the view is from the windward side.

time smaller, until finally they are mere bushes, growing singly or in groups scattered over the wet meadow areas. They are seldom much contorted, nor do they often show the effects of wind and ice crystals. Unlike the white pine, the Engelmann spruce persists in its upright habit. In its most common *Krummholz* form, as found in most parts of the cañon floors, it has a thick erect trunk a meter or two in height, and a broad flat matted crown composed of branches so tough and intricately woven that where the trees grow close together it is often possible to walk for considerable distances over their tops. Where *Picea Engelmanni* occupies more exposed positions it almost always

retains its erect habit, but the branches point to leeward of the prevalent wind. Occasionally the trunk is prostrate, but in these cases erect branches are produced, the branchlets of which are turned to leeward. There is frequently a tendency in this species, when growing, as it occasionally does, in much exposed places, to form long narrow groups of individuals, parallel to the direction of the prevailing wind, the height gradually rising from two or three decimeters at the windward end to a meter or more at the leeward end of the group. The explanation of this phenomenon evidently is that some small shelter

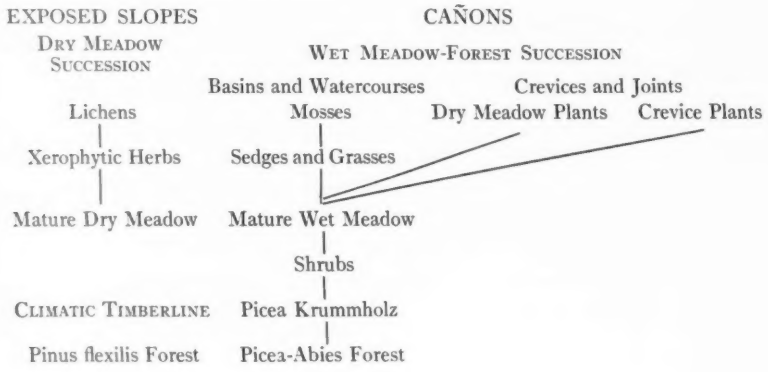
FIG. 8.—*Pinus flexilis* growing in a very exposed situation near the Long's Peak trail.

allows a seedling to live and develop into a small tree; and this gives protection in its lee to others, each of which in turn is able to rise slightly higher than the one in front. The same mode of growth is seen also in such small shrubs as *Betula glandulosa* and the low alpine form of *Populus tremuloides*, which are found in the same habitat with *Picea Engelmanni*.

Having now a general view of the forest at its upper limit, we will consider the question as to whether these two trees are at present invading the grassland. The evidence here, though it is not as complete as might be wished, points toward the general conclusion that

the forest formation is advancing in the cañons, but that on the ridges it has reached its climatic limit. The aged, battered, and twisted white pines, with no young trees among them, indicate a repulse in the effort of the forest to ascend the ridges; while, on the other hand, the gradual decrease in height, the scattering of individuals and groups in advance of the main mass, suggest that in the cañons the forest is still advancing—that it has not yet reached the point where tree growth is climatically excluded. HARVEY[4] has cited a similar condition in evidence that the forest is not climatically excluded from the summit of Mt. Ktaadn. It is an interesting fact in this connection that the Picea *Krummholz* in the cañons of the Long's Peak region bears a striking resemblance, in type of trees represented, in the *Krummholz* form which they take, and in the manner of their seeming advance, to the mesophytic Picea-Abies *Krummholz* of the eastern mountain.

It will be well at this point to recall the fact that the agency most important in preventing tree growth is dry wind during frosty weather, since it accelerates transpiration to a high degree, while the frozen condition of the ground prevents a renewal of the water supply.[5] The conditions in the Long's Peak region—the permanent timberline on the exposed ridges and the advancing forest in the sheltered cañons—agree perfectly with this theory.



[4] HARVEY, LEROY H., *Op. cit.*

[5] KIHLMAN; referred to by SCHIMPER, Plant geography 78.

C. THE SUCCESSIONS

In this study we have endeavored to trace in a general way the stages through which the vegetation of the alpine region has passed. It remains only to bring into an orderly arrangement the successions and their stages which have been described. This may best be done by means of the foregoing diagram, which in the light of what has gone before will need no further explanation.

IV. Summary

In the retreat of the Pleistocene snow masses the unglaciated slopes and summit of the divide were first uncovered and occupied by vegetation. On these areas the xerophytic "dry meadows" of today have developed.

Owing to the slower shrinkage of the valley glaciers, invasion of new areas is still going on at the heads of the glacial cañons.

The glacial cañon as a habitat is characterized by (1) comparatively favorable atmospheric conditions, (2) restriction of surface water to limited areas, (3) dependence of the production and distribution of soil materials upon surface water.

These conditions result in a vegetation consisting of a lichen society inhabiting the dry rock surfaces for an indefinite length of time, and a wet meadow society confined to the vicinity of the drainage channels. The latter society is preceded by two groups of pioneers: one, the less important, derived from the xerophytic dry meadows, becoming established in cracks and joints of the floor; the second, mesophytic in character, invading from the lower altitudes, occupying depressions and very wet places.

The evidence at hand indicates that the forest, represented at timberline by *Pinus flexilis* on the ridges, and by *Picea Engelmanni* in the cañons, has reached its climatic limit on the ridges, being prevented from further advance by the dry winter winds; but that in the cañons the forest is still invading the wet meadow society.

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Baltimore

BRIEFER ARTICLES

VARIATION IN HELIANTHUS

In a recent number of this journal, Dr. GEORGE H. SHULL[1] calls attention to the dark disk found in the wild sunflower of the prairie region, but shows that certain material received from that region was heterozygous with a yellow disk recessive. It may be worth while to report that this wild plant does actually produce a yellow-disked variety, which I have observed both in Colorado and New Mexico. The western sunflower, according to RYDBERG, is separable as a distinct species, *Helianthus lenticularis* Dougl. This seems to be going too far, and I think it should be called *H. annuus lenticularis*. The color of the disk is considered a specific character in Helianthus; but it certainly varies within specific limits, not only in *H. annuus*, but in *H. petiolaris* also, as I have shown in *Nature*, June 19, 1902, p. 174.—T. D. A. COCKERELL, *Boulder, Colorado.*

ENDOSPERM OF PONTEDERIACEAE

(WITH FOUR FIGURES)

In a recent paper[2] on the seeds of Pontederiaceae, COKER makes some references to my paper published in 1898,[3] to which I wish to make a brief reply. He says: "Oddly enough he completely overlooked the interesting peculiarity in the endosperm of all three genera." The reason for my overlooking such a peculiarity is clear enough, as a very casual reading of the paper will show that I made no attempt to follow endosperm formation. My study was based chiefly on Eichhornia, and in that genus, as grown in Washington Park, Chicago, the endosperm nucleus almost never divides, and the contents of the embryo sac disorganize without development of endosperm or embryo.

Some of my slides of Pontederia, however, extend beyond the fertilization stage, and since COKER's article appeared I have reexamined these, and am able in three cases to confirm his account of a division of the embryo sac into upper and lower chambers. *Fig. 3* shows the condition of the

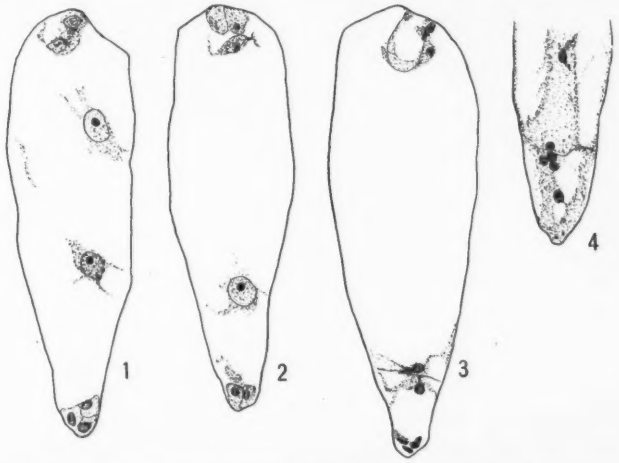
[1] Some new cases of Mendelian inheritance. BOT. GAZETTE **45**:103–116. 1908.

[2] COKER, W. C., The development of the seed in the Pontederiaceae. BOT. GAZETTE **44**:293–301. *pl. 23.* 1907.

[3] SMITH, W. R., A contribution to the life history of the Pontederiaceae. BOT. GAZETTE **25**:324–337. *pls. 19, 20.* 1898.

embryo sac just after the division of the endosperm nucleus, and *fig. 4* the lower end of the sac a short time later, with several nuclei in the lower chamber. Of later conditions of the endosperm my slides do not furnish examples.

Again COKER says: "The antipodals never divide, but they are not ephemeral as described by SMITH." There may be some difference of opinion as to what degree of persistence my description implies, but after a reexamination of my slides, and even from COKER's own figures, I am still convinced of its correctness. COKER makes the error of regarding the antipodals as a group of nuclei; he cites the persistence of such nuclei after

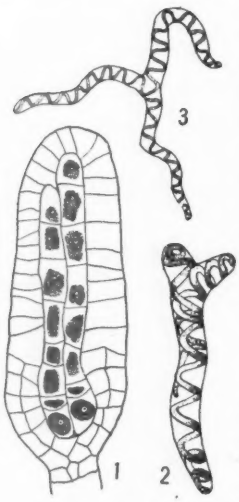


the initiation of endosperm formation as a disproof of my statement; but the antipodals are cells, not nuclei. In those embryo sacs in which they are recognized as typically persistent, such as numerous Ranunculaceae, Sparganium, and others, they become a conspicuous mass of cells; they do not persist as free nuclei. In the case of Eichhornia and Pontederia they are organized cells at the stage shown in *figs. 1* and *2* herewith, and in *fig. 13* of COKER's plate. These cells disorganize immediately after the fusion of the polar nuclei, sometimes even earlier, a behavior which amply justifies my describing them as ephemeral. In later stages of the embryo sac only the nuclei can be distinguished, and these in a partially disorganized condition, as in *figs. 3* and *4*. Compare also COKER's *figs. 13, 15, 17*, in which the disintegration of the antipodal cells and the absorption of their nuclei may be clearly traced.—R. WILSON SMITH, *McMaster University, Toronto, Canada.*

AN ABNORMAL *PORELLA PLATYPHYLLA*

(WITH THREE FIGURES)

In examining some material of *Porella platyphylla* I found one archegonium which differed in internal structure from any thus far observed.[4] This internal difference consisted in the presence of two perfectly formed egg cells, each with a row of canal cells (*fig. 1*). There were also two ventral canal cells. One row of the canal cells, as will be seen from *fig. 1*, was somewhat shorter than the other; the number of cells in each, however, was the same. The egg cells with the canal cells taken together occupied a somewhat larger space than is usual in this plant. The archegonium shown here was larger than those usually found. The two egg cells and canal cells were only clearly seen when lying in the plane shown in figure. If the archegonium was viewed at right angles to this position, they were difficult to see. This specimen was gradually brought into a strong solution of glycerin and allowed to become clear; it was then drawn with a camera lucida.



Porella platyphylla also often shows branched elaters.[5] *Fig. 2* shows one slightly branched at the end; *fig. 3* shows a more pronounced instance of such branching. In some elaters branching of the larger branches was noticed, which formed a rather complicated figure. The spiral thickenings were often very difficult to follow with certainty at the point of branching. *Fig. 2* shows their arrangement in one specimen.—F. M. ANDREWS, *Leipzig*.

[4] See also: COKER, W. C., On the occurrence of two egg cells in the archegonium of Mnium. BOT. GAZETTE **35**:136. 1903.

BLISS, MARY C., On the occurrence of two venters in the archegonium of Polytrichum. BOT. GAZETTE **36**:141. 1903.

LYON, HAROLD L., Polembryony in Sphagnum. BOT. GAZETTE **39**:365. 1905.

GOEBEL, K., Homologien in der Entwicklung männlicher und weiblicher Geschlechtsorgane. Flora **90**:277. 1902.

[5] See also: CAMPBELL, D. H., Mosses and ferns. 2d ed. 1905.

CURRENT LITERATURE

BOOK REVIEWS

Warming's textbook

In 1880 Dr. EUG. WARMING published his *Lehrbuch der allgemeinen Botanik*, which was followed by revised editions until the fourth appeared in 1901. In that edition he associated with himself Dr. W. JOHANNSEN, who elaborated the sections on the cell and on physiology.

This fourth edition has been translated into German by Dr. E. P. MEINECKE,[1] with the collaboration, in two chapters, of Professor JOHANNSEN, who has taken occasion to revise these in part. Other slight changes have been introduced by MEINECKE. But the book cannot be up to date, because, first, it is based on an edition dated 1900–1, and second, the printing of the first part, issued late in 1907, began in 1904. This delay in publication the publishers apologize for, and exonerate themselves, without saying to what it is due. The second part, about one-third the dimensions of the first, was promised before the end of 1907, but at this writing (March 2) has not been received.

The first five sections deal with what we should call the general morphology of plants. Their titles are: 1, The internal and external form of plants; 2, External morphology of higher plants, nutritive organs; 3, The plant cell and its constituents; 4, Histology; 5, Anatomy of the root, stem, and leaf. Sections on reproduction, including discussion of the flower, inflorescence, fruit, seed, relation to habitat, and evolution, are to follow in the second part.

The term morphology is much restricted by these authors, who hold that it concerns itself merely with the origin, development, and form of the external features of the plant body. However, under whatever head they are embraced, these chapters are well written, and the illustrations, mostly not original, are well selected.

The physiology, to which two long sections (180 pp.) are devoted, is in general of the formal type, though with a peculiar distribution of emphasis (as was to be expected), there being a strong tinge of ecology. The section on metabolism begins with a discussion of respiration as an exchange of gases, and makes much of the respiratory quotient; has little to say of the physical processes of exchange between the plant and the external medium, but gives much attention to the relations of plants to each other and to other organisms. The chapter on movement is too brief for anything but an exposition of the fundamental features.

[1] WARMING-JOHANNSEN, Lehrbuch der allgemeinen Botanik. Translated by E. P. MEINECKE. Imp. 8vo. Part I. pp. vi+480. *figs.* 444. Berlin: Gebrüder Borntraeger. 1907. *M*12.

While the book is a good one, we doubt whether, considering its handicap, there is room for it in the German market in competition with the other excellent texts which are there available.—C. R. B. and C. J. C.

The lighting of plants

For almost the entire period of his half-century of fruitful activity as a physiologist, WIESNER has been occupied with the relations of light to the functions of plants, and for the last fifteen years he has devoted his attention particularly to the relation of light to the plant *as a whole*. This relation is expressed briefly in the word *Lichtgenuss*, a word impossible of translation. On that account he has suggested the less happy *photolepsy* (in English "light-catching"); for "lepsy" lacks the idea of limits set by satisfactoriness that is involved in *Genuss*. WIESNER has now brought together in book form an easily comprehensible synopsis of the results of his long study, carried on in many and diverse regions.[2] It would be a mistake, however, to suppose that the book consists of extracts from earlier works, on which confessedly it is based. In it a considerable number of researches are now first published, especially those on the specific green of the leaves of woody plants as related to their illumination. Also new is the attempt to present a physiological analysis of *Lichtgenuss*.

The *Lichtgenuss* (L) of a plant may be expressed either relatively or absolutely. Relatively it is that part of the total daylight which reaches it. Thus if i be the intensity of light reaching the plant taken as unity, and I the intensity of the total daylight expressed in that unit, then $L=i/I$. Absolutely L may be expressed in any convenient photometric units, and to photometric methods the author devotes the first chapter of the book. These, convenient and adaptable as they are, leave still to be desired a method which will reveal more accurately the photosynthetic value of the light which falls on a plant.

The second chapter analyzes the daylight, consisting as it does of direct and reflected sunlight in varying proportions, directions, and intensities, and shows how total light may be reckoned and graphically represented through the course of a day or a longer period. In the third chapter the illumination of plants is discussed, showing how it is affected by all sorts of conditions, and how plant form is influenced by the lighting. The fourth chapter is devoted to specific observations upon the photolepsy of various types of plants in their habitats; the fifth treats of the constancy or variability of photolepsy in different stages of development, and the optima thereof; the sixth discusses the dependence of photolepsy upon latitude and altitude, and includes particularly the author's observations in this country in 1904; the seventh deals with various sorts of leaf-fall; and the eighth points out the connection of mycorhiza formation with the *Lichtgenuss*.

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[2] WIESNER, J., Der Lichtgenuss der Pflanzen. Photometrische und physiologische Untersuchungen mit besonderer Rucksichtnahme auf Lebensweise, geographische Verbreitung und Kultur der Pflanzen. 8vo. pp. viii+322. *figs. 25*. Leipzig: Wilhelm Engelmann. 1907. *M*9.

In the ninth chapter WIESNER describes the differences in tone that have often been observed in the green of leaves and connects it with the excess, deficiency, or sufficiency of the illumination, much as STAHL and JÖNSSON had done on somewhat different grounds. The tenth chapter attempts a physiological analysis of the *Lichtgenuss*, which inevitably is "up in the air." The last chapter shows how the study of light relations by the photometric methods proposed can be of service in plant culture; and how the results of such study may serve as guides to proper planting in all sorts of conditions and locations. A bibliography (4 pp.) and a double index (topics and plant names) complete the book.

While for him who wishes to carry on investigations along these lines the various memoirs that have come from WIESNER'S hand are indispensable, this book will better serve one who desires merely a general statement of results and principles. At the same time it must be said that the book contains much that is wholly familiar and commonplace, so that it might have been much condensed to advantage; but perhaps the picture would not have been so complete. Furthermore, the book is by no means free from doubtful generalizations and generous assumptions; indeed, it seems that everyone who deals with adaptations must allow his imagination a rather loose rein. Withal there is in the work an important nucleus of no little value, and even an occasional flight of fancy may be permitted, if it stimulate interest.—C. R. B.

MINOR NOTICES

Cryptogamic flora of Brandenburg.[3]—The second part of the volume on Algae, by LEMMERMANN, has now appeared. It concludes the Oscillatoriaceae; includes Nostocaceae, Microchaetaceae, Scytonemataceae, Stigonemataceae, Rivulariaceae, and Camptotrichiaceae; and begins the Flagellatae.—J. M. C.

List of British plants.—DRUCE[4] has published a list of British plants, including the "Spermophytes, Pteridophytes, and Charads," found either as natives or growing in a wild state in Britain, Ireland, and the Channel Isles. The introduction contains a protest against the *nomina conservanda* of the Vienna Congress, and these are "deliberately ignored." The list is especially for "working botanists and members of the exchange clubs." The census of species shows 1390 native species, 144 alien species now well established, and 940 more or less fugitive aliens, the total enumeration including 2964 numbers.—J. M. C.

Trees and shrubs.—A preliminary announcement of SARGENT'S *Trees and shrubs* appeared in this journal in 1902, and there followed notices[5] of the four parts which completed the first volume in 1905. The first part of the second

[3] LEMMERMAN, E., Kryptogamenflora der Mark Brandenburg, Band 3, Heft 2. Algen. pp. 129–304. Leipzig: Gebrüder Borntraeger. 1907. Algen (Band 3, Heft 1 u. 2). *M* 9.50.

[4] DRUCE, GEORGE CLARIDGE, List of British plants. pp. xv + 104. Oxford: Clarendon Press. 1908. 2*s*. 6*d*.

[5] BOT. GAZETTE **34**:388. 1902; **35**:62. 1903; **36**:68. 1903; **37**:155. 1904; **39**: 372. 1905.

volume has now appeared.[6] The twenty-five species illustrated include six new species of Crataegus from Missouri, and new species from China or Japan under Ulmus, Berberis, and Viburnum (3). Four new species of Lonicera from China are described without illustration by REHDER, who also describes and illustrates a new hybrid under Malus. The tropical American (Florida and Mexico to Central America) species illustrated are *Alvaradoa amorphoides* Liebm., *Pinus Greggii* Engelm., and *P. Lumholtzii* Robinson and Fernald. The ten remaining species are from China or Japan, and belong to Berberis, Acer, Rhododendron, Viburnum (5), and Lonicera (2).—J. M. C.

Plant phyla.—Professor BESSEY[7] has been working for many years upon a natural (evolutionary) classification of plants, and the result has just appeared in published form. He recognizes fifteen great "phyla," and presents a diagram to illustrate their relationship. It is impossible to give any adequate conception of the scheme, for it is very compactly presented and includes an enormous mass of details. A glimpse of the point of view may be obtained from the following list of the "phyla," the number following each name indicating the number of families included: Myxophyceae (9), Protophyceae (17), Zygophyceae (21), Siphonophyceae (18), Phaeophyceae (23), Carpophyceae (26), Carpomyceteae (145), Bryophyta (54), Pteridophyta (13), Calamophyta (4), Lepidophyta (7), Cycadophyta (9), Gnetales (1), Strobilophyta (9), Anthophyta (280). The labor involved in organizing and defining these 636 families must have been enormous.—J. M. C.

American Breeders' Association.—The literature of breeding which is now growing with great rapidity is necessarily much scattered. The third annual report of the American Breeders' Association[8] contains a large number of papers covering a wide range of subjects relating to both plant and animal breeding. The papers which are of most interest to scientific breeders and students of heredity are "Inheritance in pedigree breeding of poultry" and "Recent advances in the theory of breeding," by C. B. DAVENPORT; "The production and fixation of new breeds," by W. E. CASTLE; "Some results in selecting red clover for disease resistance," by S. M. BAIN; "Heredity in carnation seedlings," by J. B. NORTON; "Report of the committee on theoretic research in heredity," by CHARLES W. WARD; "The chromosome in the transmission of hereditary characters," by W. J. SPILLMAN. There are also a number of excellent papers and reports which must be of the greatest value to breeders of the economic crops. One of the best of these

[6] SARGENT, C. S., Trees and shrubs. Illustrations of new or little known ligneous plants, prepared chiefly from material at the Arnold Arboretum of Harvard University. Vol. II. Part I. pp. 1–55. *pls. 101–125.* Boston and New York: Houghton, Mifflin & Company. 1907. $5.00.

[7] BESSEY, CHARLES E., A synopsis of plant phyla. Univ. Nebraska Studies **7**:no. 4. pp. 100. 1907. Lincoln: University Publishing Company. 50 cents.

[8] Annual report of the American Breeders' Association, Vol. 3. 8vo. pp. 305. Washington, D. C. 1907.

is a scheme for corn breeding worked out in very clear detail by C. G. WILLIAMS, by which it is hoped to secure the greatest possible improvement without encountering the injurious effects of inbreeding. In the rapid development of all breeding problems, due to the universal interest which is being taken both in scientific and economic aspects of the subject, the annual reports of the American Breeders' Association must continue to be a most valuable source of information as to the present state of knowledge, and no one who is interested in these problems from either point of view can afford to be without the annual volumes.—GEORGE H. SHULL.

NOTES FOR STUDENTS

Ascent of water.—EWART becomes a stronger and stronger opponent of the DIXON-JOLY theory of the ascent of sap, and in his last paper[9] adduces some powerful arguments, backed by observations, against it and in favor of the theory of vital maintenance of suitable conditions for conduction and some sort of pumping action. The latter may be by surface tension, but while theoretical ways abound in which this might be applied, no practical proof of the existence of any such action in wood is forthcoming. EWART'S experiments all tend to show, he thinks, that the continuous ascent of water is possible only in living wood, and that the power of conduction is rapidly lost at death. Experiments on the suction and exudation of trees at different levels showed no continuous water columns or high internal tensions in the tracheae during active transpiration, and this fact, coupled with the high total resistance to flow, indicates that this resistance is overcome locally from point to point, and not by enormous tension from above, which leads to blocking by gas bubbles, nor by pressure from below, which leads to great loss by lateral exudation from the vessels.

EWART makes several corrections of his own and others' previous observations. He finds no vessels open the whole length of the tree, as STRASBURGER thought to be the case in oak. Wistaria furnished him the longest—5.64^{m}. In the oak they are seldom over 1^{m}. Nor does EWART sustain STRASBURGER'S results on the conduction of water through dead wood, for if these experiments are sound, vital action is out of the question. His own earlier observations on the osmotic pressures in leaves at different levels are also disowned, for he now finds as great differences in leaves at the same level. Incidentally he looked up the evidence as to the height of the tallest trees in Australia, and concludes that none appreciably exceed 300 feet, instead of being 472 as reported. He thinks that the height of some of our American big trees may likewise shrink on investigation.

In the course of the discussion of exudation he makes the very good point that fully turgid cells, for example, those of the root cortex, may act simply as a membrane between the water in the vessels and the outside water, their own osmotic pressure, however high, having no influence on the transfer of water from soil to vessel so long as they remain fully turgid. This also explains how cells of unlike

[9] EWART, A. J., The ascent of water in trees (second paper). Phil. Trans. Roy. Soc. London B **199**:341–392. 1908.

osmotic pressure can exist side by side without those of higher pressure draining those of lower, which, however, they would do as soon as their turgor was relaxed ever so slightly, thus releasing some of the osmotic energy that had previously been expended against the wall. This point has been often overlooked.

URSPRUNG[10] makes what he himself properly calls "a small contribution" (which nevertheless fills sixty-odd pages!) to a more extended study of the relation of live cells to the ascent of water in woody plants. His data will be more useful than his interpretation. The experiments, carried on in the forests, embraced five species of gymnosperms and fifteen of angiosperms. The axes were killed for greater or less distances at various levels by steam, and usually others were girdled at the same time. Microscopic examination was made of both dead portions and neighboring parts. URSPRUNG explains the dissimilar behavior of different species on the assumption (and therefore begs the question) that the experimental interference eliminates the vital component of the lifting forces, but does not affect the physical; so as the vital factor is greater or less the wilting of the leaves occurs in a few days in some experiments or is delayed to 100 in others. His "results" he summarizes thus: "In all the plants investigated a participation of the living cells in the production of the lifting force is to be assumed." (Is this a *result?*) "Water conduction occurs chiefly in the younger layers of the wood." (This has been long known.) "In all observed plants the cortex must be present in order to make possible the continuance of a sufficient water movement; its removal acts injuriously, though not everywhere equally. The significance of the cortex for the ascent of sap lies probably in its protective function for the periphery of the wood." (This has scarcely been doubted.) "For a sufficient water-movement a small fraction of the conducting tissues suffices, if in the part remaining the wood cells be living." (The *if* is not a condition proved but assumed.) "The force component arising from the living cells attains great significance in comparison with the purely physical." (*Quod est demonstrandum.*) —C. R. B.

Items of taxonomic interest.—C. B. CLARKE (Contrib. U. S. Nat. Herb. **10**:443–471. 1908), before his death, had prepared a synopsis (in Latin) of the Cyperaceae of Costa Rica. This has now been published, with such changes as were necessary, such as translation into English (by E. L. GREENE), rearrangement of synonymy, completion of citations, elimination of *nomina nuda*, etc. A synoptical key to the 19 genera precedes the presentation of the 105 species. The large genera are Rynchospora (16), Cyperus (15), Eleocharis (13), and Scleria (11), and a single new species is described in each of the following genera: Cyperus, Rynchospora, and Carex.—J. J. SMITH (Bull. Dept. Agric. Ind. Néerland. no. 13. pp. 78. *pls.* 2. 1907), in the first of a series of papers on the orchids of Java, has described 15 new species and 2 new genera (*Silvorchis* and *Lectandra*).—E. ULE (Notizblatt **5**: no. 41*a*. pp. 52. *pls.* 4. 1908), in connection with an account of the

[10] URSPRUNG, A., Abtötungs- und Ringelungsversuche an einigen Holzpflanze. Jahrb. Wiss. Bot. **44**:287–349. *pl.* 4. 1907.

caoutchouc industry of Bahia, has described 3 new species of Manihot.—P. B. KENNEDY (Muhlenbergia **4**:1–4. 1908) has described a new species of Dicoria from Nevada.—S. SOMMIER (Giorn. Bot. Ital. N. S. **14**:496–505. *pl. 14.* 1907) has described a new genus (*Melitella*) of Compositae (Cichoriaceae) from Malta.—R. PAMPANINI (*idem* 591–606), in describing a fascicle of new species, includes a Codonanthe from Brazil and a Sesbania from Central America (Mexico?).—A. B. RENDLE, E. G. BAKER, and S. LEM. MOORE (Jour. Linn. Soc. Bot. **38**:228–279. *pls. 16–19.* 1908), in an account of the Wollaston collection of plants from Mt. Ruwenzori (Africa), describe 34 new species, among which there is a new genus (*Choananthus*) of Amaryllidaceae.—A. D. E. ELMER (Leaflets Philipp. B **1**:212–219. 1907) has described 8 new species of Freycinetia from Lucban; also (*idem* 220–232) 11 new species of Leguminosae, including the new genus *Luzonia* (nearest Canavalia); and (*idem* 236–261) has presented 41 species and varieties of Ficus collected within a radius of three miles of Lucban (Luzon), including 6 new species.—E. B. COPELAND (*idem* 233–235) has described 3 new species of ferns from the Philippines.—J. H. BARNHART (Bull. Torr. Bot. Club **34**:579–582. *pl. 34.* 1907) has described a new Utricularia from Long Isand.—J. C. ARTHUR (*idem* 583–592), in his sixth fascicle of new Uredineae, describes 15 new species.—K. K. MACKENZIE (*idem* 603–607), has described 4 new species of Carex.—H. REHM (Annales Mycol. **5**:516–546. 1907), in describing 95 new species of Ascomycetes from various parts of the world, includes 18 from North America and 38 from South America.—In publishing the third fascicle of WEBERBAUER'S new plants from the Andes (Bot. Jahrb. **40**:225–395. 1908), 264 new species are described, including the following new genera: *Urbanodoxa* and *Englerocharis* (Cruciferae), by R. MUSCHER; *Urbanosciadium* (Umbelliferae), by H. WOLFF; and *Acrobotrys* (Rubiaceae), by K. SCHUMANN and K. KRAUSE.—R. PILGER (*idem* 396, 397) has described a new genus (*Glischrothamnus*) of Aizoaceae from Brazil.—R. SCHLECHTER (Bot. Jahrb. Beibl. **40**[3]:1–19. 1908), in describing 36 new Asclepiadaceae from the East Indies, includes the new genera *Oistonema* and *Anatropanthus;* the same author (*idem* 20–45) describes 54 new species from New Caledonia, and includes four new genera (*Dolichanthera*, *Rhopalobrachium*, *Atractocarpus*, *Bonatia*) of Rubiaceae.—C. C. HOSSEUS (Bot. Jahrb. **41**:55–61. *pls. 1, 2.* 1908) has described a new genus (*Richthofenia*) of Rafflesiaceae from Siam; he has also published (*idem* 62–73) a list of 55 species of Acanthaceae from Siam, including 12 new species.—E. KOEHNE (*idem* 74–110) has supplemented his account of Lythraceae in ENGLER'S *Pflanzenreich* (1903) by intercalating species published since that date, many of them American (chiefly Mexican), and by adding 16 new species published here for the first time.—N. L. BRITTON and J. N. ROSE (Smithson. Misc. Coll. **50**:503–539. 1908) have published a preliminary account of the Opuntioideae of North America, recognizing 143 species of Opuntia (15 of which are new), 6 of Nopalea, and 11 of Pereskiopsis, a genus recently published in the same serial (331–333).—J. M. C.

The individuality of the chromosome.—By subjecting root tips of *Pisum sativum* to a 0.75 per cent. solution of chloral hydrate at 20° C. for one hour,

then washing away the chloral hydrate in water and growing the tips in sawdust, NEMĚC found that after 20 hours many cells have become binucleate. After 27 hours few cells are binucleate, but many contain large nuclei which contain 28 chromosomes, twice the *2x* number. After 40 hours the mitoses show regularly 14 chromosomes, the *2x* number. NEMĚC believed the quadruple number to be brought back automatically to the *2x* number by a heterotypic mitosis.

STRASBURGER[11] has traversed the same ground, treating material of *Pisum sativum* in the same way and making an exhaustive study of all the cytological phenomena. He found cells with two nuclei and observed that such nuclei fuse to form large nuclei with 28 chromosomes, the quadruple number; but such mitoses, aside from the large number of chromosomes, present no striking peculiarities. There are abnormalities, due to the chloralization, but there are no characteristics of the heterotypic mitosis or anything else to indicate a reduction to the *2x* number; but rather there is evidence that the *4x* number, once established, persists.

The investigation of chloralized nuclei was made particularly exhaustive, that it might form a basis for comparison with nuclear phenomena in graft hybrids. An investigation of typical and chloralized nuclei of *Laburnum vulgare*, *Cytisus purpureus*, and *Laburnum Adami* presented rather constantly 48 chromosomes, the *2x* number, and showed no evidence of any fusion, reduction, or autoregulation. These plants gave no response to such chloralizing as that described for *Pisum sativum*, and after greater stimulation nuclear divisions were not resumed. The study of nuclear phenomena threw no light upon the problem of graft hybrids. There were no heterotypic mitoses and the author doubts whether heterotypic mitoses are to be found in vegetative or somatic tissues. Such mitoses as those described by English writers for malignant tumors STRASBURGER believes to be incorrectly interpreted.

The noted Mespilus at Bronvaux, recently studied by NOLL, is discussed, and here again there is no evidence of fusion or reduction. A study of the Bizzaria orange compared with "Agrumi," which is not a hybrid, showed no cytological differences; both have 16 chromosomes. The evidence showed that Bizzaria is a hybrid of sexual origin and that there is nothing to support any theory of autoregulation.

The paper gives a full account of the cytological details of graft hybrids, together with theoretical discussions which cannot be treated adequately in a brief review.—CHARLES J. CHAMBERLAIN.

Phototropism and perception of light.—FITTING has undertaken[12] to solve the question whether a localized tropic or nastic sensitiveness must be considered as a sign of localization of the *perceptive faculty* for the stimulus, and whether it

[11] STRASBURGER, EDUARD, Ueber die Individualität der Chromosomen und die Pfropfhybriden-Frage. Jahrb. Wiss. Bot. **44**:482–555. *pls.* 5–7. 1907.

[12] FITTING, H., Lichtperception und phototropische Empfindlichkeit. Jahrb. Wiss. Bot. **45**:83–136. 1907.

is justifiable to speak of a localized phototropic irritability as merely a localization of sensitiveness to light. For this purpose he chose seedlings of *Panicum miliaceum*, in which the tip of the cotyledon alone is phototropically sensitive, and determined how the growth in length of the part not thus sensitive was affected by direct illumination and by illumination of the cotyledon tip, preliminary investigations having shown that the growth, which is restricted almost entirely to the uppermost part of the hypocotyl, is greatly retarded, and that the amount of retardation is closely dependent upon the intensity of the light. In light of moderate intensity the growth of the hypocotyl is checked almost equally, whether the cotyledon alone or the hypocotyl alone is illuminated; but only half so much as when the whole seedling is illuminated. At higher intensities, on the contrary, the illumination of the cotyledon retards the growth more; from which it is evident that the effect of the light is transmitted downward to the hypocotyl. But if one illuminates all but the uppermost 2–4^{mm} of the hypocotyl, the growth of the parts above is not retarded, and the light effect is clearly not transmitted upward. The retarding effect of illumination of the cotyledon does not proceed from its tip, which is phototropically very sensitive, for illumination of this tip alone produces far less retardation of the growth of the hypocotyl than does the illumination of a greater part of the hypocotyl. Clearly the light acts as a stimulus and both cotyledon and hypocotyl are sensitive to it. Although, as ROTHERT has shown, the hypocotyl is in general not phototropically sensitive, FITTING found that 17–25 per cent. of the seedlings whose cotyledons were darkened curved phototropically after one-sided illumination. These facts show that the distribution of *phototropic* sensitiveness does not indicate which part of the seedling perceives light. Similar results were obtained with *Sorghum Dora*, *S. vulgare*, *Zea Mays*, and *Tinantia fugax* (Commelinaceae).

FITTING found nothing to indicate that phototropic sensitiveness proceeds from any other process of light perception than that which expresses itself in retardation of growth. He suggests "that the localization of phototropic sensitiveness may perhaps be referable to the fact that the polar condition characteristic of induction of phototropism can be produced only in the phototropically sensitive zone."

He discusses also the problem of etiolation, but adds nothing new, merely emphasizing the existing view that the normal form of leaves in dicotyls depends upon the direct action of light as a stimulus without the correlations which are usually considered.—C. R. B.

Javanese Anthocerotales.—As one of the results of his recent visit to the oriental tropics, CAMPBELL[13] has published an account of certain Javanese Anthocerotales. Among a number of species of Anthoceros collected at the base of Mt. Salak and also near Tjibodas, he found two forms which he believes should constitute a new genus, *Megaceros*, into which he would throw all the non-

[13] CAMPBELL, D. H., Studies on some Javanese Anthocerotaceae. Annals of Botany **21**:467–486. *pls. 44–46.* 1907; **22**:91–102. *pls. 9,10.* 1908.

stomatiferous species with spiral elaters. The important differences between Megaceros and Anthoceros are that the former has multiple chromatophores, no stomata, a solitary antheridium, spiral elaters, and green spores. In one species (*M. salakensis*) the sporogonium dehisces along one side. The thallus closely resembles that of Anthoceros. The reviewer has frequently observed single antheridia in *A. laevis* and the same is reported for *A. Pearsoni*. The axial row is cut out of the archegonium initial by three intersecting walls, as is true for all Hepaticae. The neck-canal cells are four, rarely five. The early development of the embryo and details of the sporogonium closely resemble Dendroceros, but the sporogenous tissue is more extensive than in either Anthoceros or Dendroceros. One figure suggests that perhaps a portion of the tip of the endothecium is sporogenous, as has been found in Notothylas by LANG. The sterile cells form an irregular network inclosing the spore mother cells, which are slightly lobed. The elaters are branched. No germ tube is produced.

Two Javanese species of Dendroceros, designated *A* and *B*, were studied. Species *A* had a better-developed columella than *B*. In a Jamaican species the reviewer finds that the tip of the sporogonium is occasionally sterile. Spores of *A* and *B*, as well as other Javanese species of Dendroceros, germinate before being shed.

Notothylas javanicus closely resembles the cosmopolitan *N. orbicularis*. The archegonia are broader than in Anthoceros, but the neck-canal cells are reduced to three. The first division of the embryo is longitudinal, and not transverse as MOTTIER thinks is true in *N. orbicularis*. It is suggested that possibly the endothecium contributes something toward sporogenous tissue, as has been recently shown in another species of Notothylas by LANG, although CAMPBELL makes no mention of LANG'S work.

CAMPBELL thinks that perhaps the affinities of the Anthocerotales are with the Marchantiales rather than with the Jungermanniales; that perhaps the sporogonium of Notothylas is best compared with that of Cyathodium. He thinks that the relationships of the group are so remote from other Hepaticae that it should form a special class, "Anthocerotes."—W. J. G. LAND.

Ever-sporting varieties and variegation.—Ever-sporting varieties have received illuminating treatment by BAUR,[14] who places the sport condition among the normal fluctuating reactions of the particular variety in question. When there is a complete parallelism between the modification of a character and the variation of external stimuli which cause the modification, a chance distribution of varieties results; but when this parallelism is only partial, as is frequently the case, a "half-Galton" or otherwise modified curve will appear, and the occurrence of such modified curves may serve as a sign of ever-sporting varieties.

The sport condition appears only when a certain intensity of the combi-

[14] BAUR, E., Untersuchungen über die Erblichkeitsverhältnisse einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*. Ber. Deutsch. Bot. Gesells. **25**:442–454. 1907.

nations of external modifying stimuli and nutritive conditions, in the widest sense, is exceeded. In each ever-sporting variety there is a critical period at which the "normal" or the "sport" condition is determined. If this period occurs late in the ontogeny, the sport appears as a partial variation, as in the five-leafed clovers; and if it is very early in the ontogeny, the variation appears to be individual, as in the case of double stocks.

A sharp distinction is drawn between these modifications and mutations, and KLEBS is criticized for failing to keep them separate. This criticism would apply equally well to many other writers.

With ever-sporting varieties, many variegate-leaved varieties have a great but purely superficial resemblance. The author recognizes two types of golden modification, one due to disease, the other hereditary. Pedigree cultures with the latter type present striking results in the case of *Antirrhinum majus pumilum fol. aureis* and *Pelargonium zonale*. In Antirrhinum the cross between any two variegated specimens gives variegated and green in ratio 2:1, of which the green breed true. The conclusion was reached that variegation is in this case a Mendelian character, in which the union of two "variegated" gametes does not give rise to a successful zygote. In proof of this view, the cross between variegated and green (DR×R) gave in every case the expected ratio 1:1. Every variegated individual is thus a heterozygote, and the problem of the "fixation" of the variegated race is the same as that of the fixation of the blue Andalusian race of fowls.

In *Pelargonium zonale* a somewhat similar situation seems to exist, but here the extracted dominants, instead of being entirely incapable of development, appear as pure-white individuals which perish very early, leaving again the ratio of variegated to green, 2DR:1R.—GEO. H. SHULL.

Injury by smoke.—Continuing the studies embodied in the volume published a few years ago on the injury of vegetation by smoke,[15] which treated chiefly of gases, HASELHOFF, with the assistance of several colleagues, has been investigating the effect of the solid constituents of smoke and other factory emanations, which fall as dust, and may injure plants either directly by contact with their leaves or indirectly through their roots by way of the soil.[16] Such investigations are particularly important in continental countries, where huge factories are often closely surrounded by cultivated fields. They are of less value in this country, where the cultivation is less close and a strong tendency exists to mass factories in industrial centers. Yet at any time such data as are here set forth may be called for as a guide for legislation, or in civil cases.

HASELHOFF finds that the dust varies much in composition even from similar fuels and the same sort of factories, so that it becomes necessary in each case to determine its composition. Chlorids (NaCl), sulfids ($NaSO_2$ and $Ca(SO_2)_2$), and perhaps also sulfates ($NaSO_4$) are particularly injurious. The sulfids are

[15] See BOT. GAZETTE **38**:148. 1904.

[16] HASELHOFF, E., Versuche über die Einwirkung von Flugstaub auf Boden und Pflanzen. Landw. Versuchs-Stat. **67**:157–205. *pls. 1, 2.* 1907.

injurious through their action upon the soil, especially if its unfavorable condition facilitates the formation of H_2S. Analysis of plants often shows them to contain an increased quantity of the constituents of the dust. Microscopic investigation of the leaves shows clearly the injurious action of various dusts, which is substantiated by tests with the component salts; but there are no typical anatomical marks by which the injury wrought by one kind of dust may be distinguished from another.—C. R. B.

Polystelic roots.—Polystely in stems, as described by VAN TIEGHEM, has been disproved, but it seems clear that the phenomenon occurs in roots. CORMACK and later DRABBLE[17] described a multistelic condition in the roots of palms, and a recent research by WHITE[18] proves its occurrence in both the lateral and the tuberous roots of certain orchids belonging to Ophrydinae. In *Habenaria orbiculata* the stele of the lateral root is at its base monostelic, farther out it flattens, becomes horseshoe-shaped, then divides into two steles which at the tip merge into a common plerome cyclinder. In *H. blephariglottis* a protostele acquires a pith and internal endodermis, then opens out to a horseshoe-shape from the free ends of which steles are constricted; as in the former case these steles merge into a common plerome at the root tip. In *H. hyberborea* the steles are separate from the start, but increase in number as they proceed farther from their origin. In the tubers the steles have a similar diffuse origin, and it was upon a study of these that VAN TIEGHEM founded his theory of "concrescence" to account for the conditions seen in orchid roots. The present research strongly supports the view advanced by JEFFREY as to the extrastelar nature of the pith, for in *H. blephariglottis* the pith of the proximal part of the central cylinder merges into the fundamental tissue of the polystele. Moreover, the plerome initials are seen to give rise to both fundamental and vascular tissues, hence HANSTEIN's theory as to the correspondence of plerome and periblem to stele and cortex respectively cannot be maintained.—M. A. CHRYSLER.

Salt marshes of New England.—The construction of an electric railroad across a salt marsh at York, Maine, recently afforded an opportunity of examining a vertical section through the deposits beneath the turf of the marsh. A study of such a section by PENHALLOW[19] shows that there was an abrupt conversion of a fresh-water bog into a salt marsh by the sudden intrusion of sea water, and that this phenomenon was connected with the gradual subsidence of the general area in which the marsh is situated. It would appear that at some former time (Pliocene) shallow basins existed between islands along the Atlantic coast, and some of these basins, being cut off by the formation of barrier reefs, were converted into

[17] Reviewed in this journal **39**:382. 1905.

[18] WHITE, J. H., On polystely in roots of Orchidaceae. Univ. of Toronto Studies, Biological Series no. 6. pp. 20. *pls. 1, 2.* 1907.

[19] PENHALLOW, D. P., A contribution to our knowledge of the origin and development of certain marsh lands on the coast of New England. Trans. Roy. Soc. Canada III. 1**4**:13–56. 1907.

fresh-water ponds by the drainage from the adjacent areas. The ponds subsequently became sphagnum bogs, with the usual succession of vegetation culminating in a white pine swamp. The weight of this forest submerged it in the quaking bog upon which it rested, killing the trees, and establishing more hydrophytic conditions. The white pines then reestablished themselves and dominated the area for a century, when the forest development was abruptly terminated by the influx of salt water caused by the subsidence of the region and the consequent breaking-through of the barrier reef. The duration of the marsh from the establishment of bog plants on the sphagnum to the present time is estimated at 420 years. —GEO. D. FULLER.

Studies in the rusts.—OLIVE has published abstracts[20] of two recent studies among the rusts. One deals with the conflicting statements of BLACKMAN and CHRISTMAN in reference to the sexual performance in the caeoma type of rusts. As a result of the study of several species of caeoma rusts, OLIVE confirms CHRISTMAN as to the fusion of two similar gametes by the development of a conjugation pore; but he also finds that the process may begin through a very small pore, so that the nucleus of the migrating protoplast may become stretched out or constricted, thus giving the appearance of BLACKMAN'S "nuclear migration." OLIVE also finds that the two gametes differ somewhat in time of development, and presents the observations on which this important conclusion is based.

The other study is concerned with the origin and relationships of the more compact, "cluster-cup" type of structure. It seems that large, irregular, multinucleate cells arise after the sexual fusion, and that the basal cells of the aecidiospore rows arise as the ultimate branches of these cells. Hence the cup structure is derived from a limited and deep-seated group of cells, and the peridium arises in consequence. OLIVE also suggests the method by which the aecidium-cup type may have originated from the simpler caeoma type, and concludes that the former type is the last member of the evolutionary series in this group.—J. M. C.

Endosperm of caprifigs.—LECLERC DU SABLON[21] has discovered that in those pistillate flowers of the caprifig in which Blastophaga has deposited eggs the endosperm develops, although fertilization has not occurred. Such endosperm he speaks of as parthenogenetic, and observes that it is digested by the larva in the same way that the normal endosperm is digested by the plant embryo, the destruction of the endosperm in both cases being complete. The parthenogenetic endosperm differs strikingly from the ordinary kind, in the absence of cellulose walls, dense cytoplasm, and very large, often irregular nuclei, which are variable in number. In the rare cases in which fertilization has occurred in a pistillate flower of the caprifig, endosperm identical with that of the "Smyrna fig" is formed, that

[20] OLIVE, E. W., The relation of "conjugation" and "nuclear migration" in the rusts. Science N. S. **27**:213. 1908.

———, The relationships of the aecidium-cup type of rust. *Idem* 214.

[21] SABLON, LECLERC DU, Structure et développement de l'albumen du caprifiguier. Rev. Gén. Botanique **20**:14–24. *pl. 6.* 1908.

is, with cellulose walls, relatively scanty cytoplasm, and small, solitary nuclei. The pistillate flowers of the caprifig in which there has been neither egg-deposition nor fertilization usually do not develop farther and become atrophied. The author thinks the conclusion to be inevitable that the "stimulus" produced by the presence of the egg and larva of Blastophaga does just what is usually accomplished by fertilization, in determining not only the development of endosperm but also the further growth of the ovule and of the pericarp, and the general form of the fig.—J. M. C.

Spore formation in Derbesia.—DAVIS[22] has published a paper treating of spore formation in Derbesia, one of the Siphonales. He studied the development of sporangia and the formation and germination of zoospores. The most interesting points of the paper are the results concerning the behavior of nuclei in the sporangium previous to the formation of zoospores. Many nuclei which do not take part in the formation of zoospores undergo degeneration. Plastids become arranged radially about the nucleus which survives the act of degeneration. Including the nucleus as a center, segmentation of protoplasm takes place to form the beginning of the zoospore; then the formation of the blepharoplast begins. Previous to the formation of the blepharoplast, the nucleus moves from near the center of the young zoospore toward the periphery. Granules around the nucleus seem to move toward the periphery, where they fuse with one another to form a ring which becomes the blepharoplast. DAVIS believes that the belepharoplast of Derbesia is not a development from the plasma membrane, but from the granules closely associated with the protoplasm investing the nucleus. The paper closes with a discussion of the cytology of the blepharoplast and the value of zoospores and gametes as taxonomic characters in Siphonales.—SHIGÉO YAMANOUCHI.

Gummosis.—RUHLAND, who had been working with the late Dr. R. ADERHOLD in the Imperial Biological Station at Dahlem upon the problem of the formation of gum, has published a preliminary paper upon the physiology of gum formation,[23] promising the full account later, with developmental and anatomical details, in the *Arbeiten* of the station. A part of the paper is devoted to a criticism of the latest theory, that of BEIJERINCK and RANT,[24] who hold that cytolytic substances issuing from the dead cells in the neighborhood of a wound cause the liquefaction of embryonal wood tissues, anomalously developed through the wound stimulus. RUHLAND, however, holds that, whenever such tissues are produced by wounding, it is the influence of the oxygen of the admitted air that determines a cessation of further division in these cells, because of the transfor-

[22] DAVIS, B. M., Spore formation in Derbesia. Annals of Botany **22**:1–20. *pls. 1, 2.* 1908.

[23] RUHLAND, W., Zur Physiologie der Gummibildung bei den Amygdaleen. Ber. Deutsch. Bot. Gessells. **25**:302–315. *figs. 3.* 1907.

[24] Wundreiz, Parasitismus, und Gummifluss bei den Amygdaleen. Centralbl. Bakt. II. **15**:366 ff.

mation of certain carbohydrates, suitable for forming the partition walls, into gums rich in oxygen. Parasites and saprophytes affect the formation of gum only by creating or enlarging rifts or wounds, hindering their recovering and recovery, and so making possible the access of oxygen. Experimental proofs are adduced for this view, whose probability is increased by many chemical considerations.—C. R. B.

Fixation of free nitrogen.—Dr. CHARLOTTE TERNETZ, baffled in an attempt to identify the pycnidial fungi which belong to the endotrophic mycorhiza of the Ericaceae, turned to a study of the ability of these fungi to fix free nitrogen when grown in N-free cultures.[25] The fungi doubtless belonged to the genus Phoma, and five species are described, derived from the roots of as many genera. These all fix atmospheric nitrogen, though in very different amounts. The three from Vaccinium, Oxycoccus, and Andromeda, while they work far less energetically in this respect than most N-fixing bacteria, nevertheless gain the largest amount of nitrogen of any known organisms in comparison with the amount of carbohydrate consumed. *Aspergillus niger* and *Penicillium glaucum* likewise are capable of fixing free N in small amounts, comparable with those yielded by the other two Phomas from the roots of Tetralix and Erica.

It may be that this action, relatively small when the fungi are grown in culture media, is much more pronounced when the mycelium grows in the cortex, and that we have here proof of the advantages which the Ericaceae derive from this association. The author's cultures show that the infection may be transmitted through the seeds and does not come necessarily from the soil.—C. R. B.

Development of leaves.—LEWIS[26] has published a second study of leaf development, in which he shows "that the basipetal and basifugal directions of growth may both occur in a single leaf; and that, although one becomes predominant, evidences of the other are apparent." In a previous paper[27] he discussed the question whether certain forms of adult leaves could be due to arrested development, "so that by comparing the mature leaves of a given plant something of their embryological history could be learned." The general conclusion is that leaves of very diverse species show a common method of leaf development, in which the basipetal and basifugal directions of growth are combined; and by the predominance of the basipetal or the basifugal elements, palmate or pinnate leaves are produced respectively. The author thinks that there is shown a determinate evolution of leaf forms, whereby diverse species tend to produce similar shapes. Plants with simple leaves constantly show tendencies toward compounding. "The persistent production of the similar forms of compound leaves which have been described is evidence in favor of determinate or orthogenetic evolution."—J. M. C.

[25] TERNETZ, CHARLOTTE, Ueber die Assimilation des atmosphärischen Stickstoffes durch Pilze. Jahrb. Wiss. Bot. **44**:353–408. 1907.

[26] LEWIS, FREDERIC T., A further study of leaf development. Amer. Nat. **41**: 701–709. 1907.

[27] Amer. Nat. **41**:431–441. 1907.

Inflorescence of Euphorbia.—Another student, SCHMIDT, has undertaken to interpret the morphology of the cyathium of Euphorbia,[28] regarding which there are nearly as many views as investigators. He considers the cyathium as an inflorescence, of unequal development in different species, in which the primary staminate flowers arise first in a spiral of $\frac{2}{5}$ divergence sometimes so low as to bring the flowers almost into a whorl. Next arise the involucral leaves (except in *E. meloformis*). The shoot which forms the primary staminate flowers branches at first dichasially; next to form *Wickeln* (perhaps also *Schraubeln*) so that the whole in the axil of an involucral leaf is a *Doppelwickel* (*Doppelschraubel*). The scales arise mostly at the base of the second and third staminate flowers of each group and are to be looked upon as their bracts. They are unequally developed, being generally larger the more open is the spiral of the involucral leaves, whose insertion is sometimes enlarged on the inside, and concrescent with the scales. The nectaries are to be considered as emergences. *E. capitulata* Rchb. is separated from the genus to form a new one, *Diplocyathium*, on account of its aberrant inflorescence.—C. R. B.

Spectrum of chlorophyll.—It is well known that the absorption bands in the spectrum of a live leaf do not correspond in position to those of a solution of chlorophyll. To account for this "displacement" two theories have been current: that the chlorophyll exists as solid particles like a precipitate in the chloroplast (HAGENBACH, LOMMELL, REINKE); or that the chlorophyll in the chloroplast is dissolved and its solvent modifies the spectrum because it has a higher dispersive power (KUNTH, TSCHIRCH). IWANOWSKI, after spectrophotometric studies, agrees with neither of these views.[29] He succeeded in producing a spectrum almost exactly like that of a live leaf by precipitating chlorophyll in strong alcoholic solution by diluting with water and adding a few drops of $MgSO_4$. On this and other grounds he concludes that the spectrum due to the light reflected from the chloroplasts themselves superposed on the true absorption spectrum produces the displacement, which increases with the size of the granules. This resembles in fundamentals TIMIRIAZEFF'S hypothesis of 1872.—C. R. B.

Morphology of Aspergillus.—FRASER and CHAMBERS,[30] in a study of *Aspergillus herbariorum*, reach the following conclusions. The conidiophores are multinucleate, and each conidium contains about four nuclei. The female organ consists of a septate stalk, a one-celled ascogonium, and a one-celled trichogyne, all of which are multinucleate. The antheridium is a small, long-stalked, multinucleate cell which either fuses with the tip of the trichogyne or degenerates before reaching this stage. Normal fertilization probably occurs in some cases, and

[28] SCHMIDT, H., Ueber die Entwicklung der Blüten und Blütenstande von *Euphorbia* L. und *Diplocyathium* n. g. Beih. Bot. Centralbl. **22**[1]:21–69. *pls. 2–5.* 1907.

[29] IWANOWSKI, D., Ueber die Ursache der Verschiebung der Absorptionsbänder in Blatt. Ber. Deutsch. Bot. Gesells. **25**:416. 1907.

[30] FRASER, H. C. I., and CHAMBERS, H. S., The morphology of *Aspergillus herbariorum*. Annales Mycol. **5**:419–431. *pls. 11, 12.* 1907.

in others it is replaced by a fusion of ascogonial nuclei in pairs. After either process the ascogonium becomes septate, and each of its cells gives rise to ascogenous hyphae. In the ascus two nuclei fuse, and three successive divisions result in eight spores, which subsequently become multinucleate. The authors regard Aspergillus as a primitive type of Ascomycetes, from which most of the others can be derived; and suggest that the Ascomycetes are related to the Basidiomycetes and the Florideae.—J. M. C.

Adventitious buds in leaves of Gnetum.—In plants of *Gnetum Gnemon* L., grown in a hothouse of the Botanic Garden at Utrecht, the tips of the leaves regularly produced adventitious buds. VAN BEUSEKOM[31] finds that these buds are formed as a result of the attacks of a scale insect, *Aspidirtus dictyospermi* Morg., a species with a world-wide distribution in the tropics and in hothouses. The punctures of this insect result in yellow vesicles at various points on the leaf, and one or more near the apex stimulate the development of endogenous callus buds. The author "explains" the appearance of the buds in the apical part alone of the leaf, by assuming that "the small wound causes an afflux of nutrient matter in an apical direction," and that this necessarily stops just beyond the apical wounds. Of course this is a mere assumption, the like of which is often made, but it would puzzle any of those who use it to show how "an afflux of nutrient matter" could occur before growth actually begins.—C. R. B.

Conjugation and germination in Spirogyra.—An examination by TRÖNDLE[32] of several thousand zygospores, some sectioned and some observed entire, confirmed the current account that the two nuclei remain separate for some time after the zygospore is formed. In *Spirogyra communis* the sexual nuclei fuse two or three weeks after the formation of the zygospore. Two successive mitoses giving rise to four nuclei, and a subsequent fusion of two of these nuclei as described by CHMIELEWSKI, do not occur. The male chromatophores in the zygote disorganize in about fourteen days after conjugation, leaving only the chromatophores of the female gamete. The writer also talks about a reduction of the hereditary mass, referring to the nuclear material, but nothing in the text or figures indicates any counting of chromosomes or any study of the mechanism of reduction. The paper contains a detailed account of the chemical changes occurring during the development of the zygospore.—CHARLES J. CHAMBERLAIN.

Plantae Lindheimerianae.—To students of the Texan flora ENGELMANN and GRAY'S *Plantae Lindheimerianae*, in two parts, is a classic. It now appears that all of the collections of this pioneer botanist were not published and distributed, and the rich remnant came into the possession of the Missouri Botanical Garden

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[31] VAN BEUSEKOM, JAN, On the influence of wound stimuli on the formation of adventitious buds on the leaves of *Gnetum Gnemon* L. Recueil Trav. Bot. Néerl. **4**:pp. 27. *pls.* 3. 1907.

[32] TRÖNDLE, A., Ueber die Kopulation und Keimung von Spirogyra. Bot. Zeit. **65**:188–216. *pls.* 5. 1907.

with the ENGELMANN herbarium. This unpublished and undistributed material, containing about 650 numbers, represents the collections of 1849–1851, and proves to be very valuable. It has now been published by BLANKINSHIP,[33] who has still further added to the value of the contribution by including also the numbers of the earlier fascicles not previously enumerated (*Plantae Lindheimerianae* having been left unfinished at the end of the Compositae); a bibliography of Texan botany; a complete index of all three parts, with modern equivalents and corrections, the nomenclature comforming to the Vienna code; and a most interesting sketch, with portrait, of "LINDHEIMER, the botanist-editor," from data largely supplied by his son and daughter.—J. M. C.

Mutation and geographic distribution.—WILLIS[34] has continued his arguments in favor of mutation by analyzing the geographic distribution of the Dilleniaceae, stating that this family is chosen simply because it is the first family in HOOKER'S *Flora of British India* "with other than world-wide distribution." The details of the analysis cannot be given here, but the results are intended to show that the theory of mutation greatly simplifies the problems of geographic distribution.

In another short paper[35] WILLIS suggests what seems to be an important consideration in the origin of species of flowering plants, namely, that "while the characters that distinguish species and genera are largely characters of the floral organs, the struggle for existence is almost entirely among the seedlings and young plants, in which these organs are not yet present."—J. M. C.

Fertilization in Polytrichum.—The VAN LEEUWEN-REYNVAANS[36] have published the first account of the details of fertilization in mosses and describe most remarkable behavior by the chromatin. In the next to the last division of the spermatogenous cells each daughter nucleus receives six chromosomes, but in the final mitosis only three, so that the sperm contains only three chromosomes. The mitosis which forms the egg and ventral canal cell shows only three chromosomes for each nucleus. The egg and ventral canal cell become pressed together and their nuclei fuse, forming a nucleus with six chromosomes. Two sperms then unite with this egg, thus restoring the sporophytic number of chromosomes, which was found to be twelve. The full paper with the plates will be awaited with interest.—CHARLES J. CHAMBERLAIN.

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[33] BLANKINSHIP, J. W., Plantae Lindheimerianae, Part III. Ann. Rep. Mo. Bot. Garden **18**:123–223. 1907.

[34] WILLIS, J. C., The geographical distribution of the Dilleniaceae, as illustrating the treatment of this subject on the theory of mutation. Annals Bot. Gard. Peradeniya **4**:69–76. 1907.

[35] Further evidence against the origin of species by infinitesimal variations. *Idem* 17–19.

[36] VAN LEEUWEN-REYNVAAN, Mr. and Mrs. Doctors, On a double reduction of the number of chromosomes during the formation of the sexual cells and on a subsequent double fertilization in some species of Polytrichum. Koninklijke Akad. Wetenschappen **1907**:359–365.

Nutrition of aquatics.—A new investigation of this subject has been published by SNELL.[37] So far as the author's experiments overlap those of the reviewer, there is perfect agreement in the conclusion that aquatic plants rooted in the soil take nourishment therefrom, and that the roots function as regular organs for the entrance of food substances. In the case of *Pistia Stratiotes* the roots, though not attached to the soil, still function as roots in allowing food substance in the water to enter. The roots of Lemna, however, serve only to balance the plant. Some results were obtained which do not agree with those obtained by the reviewer, the value of which he is not willing to concede; but since the author does not regard the differences of enough importance to state them formally in the final conclusions, further discussion is not necessary.—RAYMOND H. POND.

A new pteridosperm.—ARBER[38] has described a new Pteridosperm (*Carpolithus Nathorsti*) from the coal fields of Germany, from a specimen preserved in the collections of the Swedish Academy at Stockholm. The seeds are extraordinarily small, the average length being about 1^{mm}, and the greatest width 0.75^{mm}. They are borne upon an undoubted sphenopterid frond, and were probably inclosed in cupules. It is not certain that this seed is a true Lagenostoma, but it confirms strongly the habit of the fertile fronds inferred for the species of Lagenostoma.—J. M. C.

Wound tissues.—In a somewhat lengthy discussion of wound tissues resulting from removing rings of cortex from twigs, KRIEG[39] finds that in plants growing in the sun greater masses of wound tissue are produced than in plants growing in the shade; and that in forms with larger leaves the callus above the ring is much larger than that produced by small-leaved forms.—W. J. G. LAND.

Economy of chlorophyll proper.—STAHL suggests[40] that the earlier disappearance of the blue-green component of chlorophyll, leading to the yellowing of leaves in autumn (which is checked by preventing migration of materials from the leaf or any part of it), as well as its later appearance in seedlings of etiolated plants, is a matter of economy.—C. R. B.

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[37] SNELL, KARL, Untersuchungen über die Nahrungsaufnahme der Wasserpflanzen. Flora **98**:213–249. 1907.

[38] ARBER, E. A. NEWELL, On a new Pteridosperm possessing the Sphenopteris type of foliage. Annals of Botany **22**:57–62. *pl. 6.* 1908.

[39] KRIEG, AUGUST, Beiträge zur Kenntniss der Kallus- und Wundholzbildung geringelter Zweige und deren histologischen Veränderungen. pp. 68. *pls. 25.* Würzburg: A. Stuber. 1908.

[40] STAHL, E., Ueber das Vergilben des Laubes. Ber. Deutsch. Bot. Gesells. **25**:530–534. 1907.

NEWS

THE UNIVERSITY OF WASHINGTON will open its marine station at Friday Harbor on June 22 for a session of six weeks. Dr. R. B. WYLIE, University of Iowa, will be in charge of the botany. The station is in the heart of an evergreen forest in the winter rainbelt, and the marine plants are extraordinarily abundant. The university has also announced a botanical field trip to Alaska, under the direction of Dr. T. C. FRYE, to leave Seattle about July 1, to go as far north as Skagway, and to continue for six weeks.

A FRENCH *Dictionary of botany* is in preparation by GASTON BONNIER, professor of botany at the Sorbonne, with the assistance of EDOUARD GRIFFON, professor of botany in the National College of Agriculture at Grignon and adjunct-director of the Paris Station for plant pathology, HENRI COUPIN, director of the botanical laboratory at the Sorbonne, and RENÉ VIGUIER, preparator at the Museum of Natural History. It is to include taxonomy, geographical distribution, morphology, physiology, ecology, pathology, paleobotany, agriculture, horticulture, industrial and commercial applications of botany, mythology, etymology of names and terms, and historical, biographical, and bibliographical information, all in two volumes of about 2000 pages, illustrated by more than 10,000 figures. How so comprehensive a scheme can be realized within these limits remains to be seen, but the French—publishers and authors alike—are master-hands at encyclopedic work. Publication will not be begun until the manuscript is complete, insuring regular issue of the parts.